

NITROGEN RESOURCE ANALYSIS AND MODELLING OF AN  
EELGRASS (*ZOSTERA MARINA* L.) MEADOW IN IZEMBOK LAGOON, ALASKA

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EELGRASS (*ZOSTERA MARINA* L.) MEADOW IN IZEMBEK LAGOON, ALASKA

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## ABSTRACT

Nitrogen limitation in beds of eelgrass, *Zostera marina* L., was examined by correlating plant standing stock and sediment nitrogen supplies, by measurement of nitrogen uptake in eelgrass roots and leaves, and by experimental manipulation of plant-nitrogen interaction. Eelgrass standing stock and sediment nitrogen across an eelgrass meadow were analyzed. Correlation was found between the integrated interstitial ammonium pool and shoot density and other morphological characteristics.

A model of eelgrass growth predicted the effect of nitrogen utilization on biomass production and growth rates; nitrogen limitation controlled growth throughout the summer in ammonium-poor eelgrass beds but only at the peak growth periods in ammonium-rich areas. Prediction of nitrogen enrichment effects similar to literature findings confirmed the impact of nitrogen limitation. Simulation of the spatial and seasonal influences of nitrogen and light as controls on eelgrass growth demonstrated the recurrent effects of dominant environmental limitations within an eelgrass meadow.

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*It lay,  
as a carpet of bread upon the sea  
and as it consumes,  
it is consumed.  
Such is  
its eternity!*

*Thomas Paul Sledge*

## CHAPTER 1: INTRODUCTION

A major concern of biological and ecological studies relating to plant growth is the analysis of plant nutrition. In most marine systems this problem is simplified because phytoplankton acquire all their nutrients from seawater. The situation for marine vascular plants rooted in the sediment is more complex; nutrition for these plants can come from the water or the sediments.

Eelgrass, *Zostera marina* Linnaeus, is a submerged marine angiosperm growing extensively in the shallow coastal waters of the northern temperate oceans. A monocotyledon from the large family of aquatic plants, the Potamogetonaceae, eelgrass is a flowering plant which uses its moving water medium to aid in pollination and seed dispersal. As a vascular plant rooted in sandy or mud substrate, eelgrass typically reproduces vegetatively as well as sexually.

My research evaluates the importance of nitrogen sources to the growth of eelgrass and uses this information in a simulation model for the analysis of nitrogen resource utilization in eelgrass beds. The specific problem addressed is whether during any part of the year nitrogen is limiting to the growth of eelgrass in eelgrass beds having various environmental conditions.

Nitrogen resources necessary to satisfy the growth requirement of this highly productive seagrass are available in both the water column and the sediment; however, the extent to which eelgrass can utilize these nitrogen sources was not previously completely defined. A detailed study of nitrogen kinetics was designed to investigate uptake by eelgrass leaves and roots. Analysis of nitrogen kinetics and plant

requirements in conjunction with measurements of the quantity of nitrogen available in the environment provided information needed to model nitrogen utilization in eelgrass beds. The distribution of nitrogen across an eelgrass meadow and the seasonal nitrogen supply were important factors in this assessment of resource availability.

The nature of the eelgrass ecosystem and the importance of this and other seagrasses to the ecology of coastal waters has recently been reviewed (McRoy and Helfferich 1977; Phillips and McRoy 1980). Survey studies including eelgrass distribution and seasonal biomass have illustrated similar patterns of growth across its geographic range (McRoy 1966 and 1970; Harrison and Mann 1975; Sand-Jensen 1975; Short 1975; Jacobs 1979; Aioi 1980; Mukai *et al.* 1980). These studies describe both vast eelgrass meadows and localized eelgrass beds, which grow from the extremes of the exposed intertidal zone to subtidal areas.

Experimental work with eelgrass plants has led to a basic understanding of the physiology of primary production (McRoy 1974; Drew 1979). Environmental effects on eelgrass production have also been examined through experimental studies. Reduction of incoming irradiance by shading caused a decrease in eelgrass growth (Burkholder and Doheny 1968; Short *et al.* 1974; Backman and Barilotti 1976; Dennison 1979). The effect of current velocity, previously thought to influence eelgrass growth (Conover 1968), was recently questioned after extensive experimental studies (Fonseca and Thayer 1979). Furthermore, eelgrass growth was found to increase after the *in situ* addition of nutrient fertilizer to eelgrass beds (Orth 1977).



The rapid accumulation of plant biomass in many of these experiments, and the measured eelgrass growth rates, suggest a high primary production comparable to the range of production rates for agricultural crop plants (McRoy and McMillan 1977). High production of farm crops, however, is supported by addition of nutrient fertilizer; in eelgrass beds, maintaining this high production requires a large natural nutrient resource. Two major sources of phosphorus and nitrogen are readily available to eelgrass plants: the ambient concentration in the water column, and the nutrients in the sediment interstitial water.

Phosphorus can be taken up by eelgrass from the water and from the sediments; however, the much greater concentrations in the interstitial water suggest that the sediments are a major source of phosphorus for the plants (McRoy and Barsdate 1970; McRoy *et al.* 1972a). Experiments on nine freshwater aquatic macrophyte species have shown quantitatively that these plants obtain all their phosphorus from the sediments (Cargnan and Kalff 1979, 1980). In addition, these phosphorus uptake experiments have shown that aquatic plants are a potential pump of phosphorus from the sediments into the water column. Thus from these uptake studies and knowledge of phosphorus availability in Izembek Lagoon, it appears that this nutrient is rarely limiting to eelgrass growth.

The importance of sediment nitrogen to the growth and development of eelgrass beds was alluded to in early eelgrass studies (Philip 1936). The utilization of this nitrogen resource has been demonstrated for the tropical seagrass *Thalassia testudinum* (Patriquin 1972) and the temperate *Zostera marina* (McRoy and Goering 1974). An outcome of both

these studies was the suggestion that nitrogen from the sediments supplied virtually all the nitrogen necessary for plant growth. However, in my studies (Chapter 4) and those of Iizumi (1979), both the water column and the sediment nitrogen were found to be important sources of nitrogen.

The status of research on seagrass nutrition was reviewed in 1973 at the International Seagrass Workshop in Leiden, The Netherlands (McRoy 1973). Many recommendations for further investigation set forward at that workshop are addressed in this thesis. Among these, a detailed discussion of the nitrogen available for plant production and an index for assessing the nutrition level in the sediments are presented in Chapter 2. The available nitrogen resources drive the kinetics of the plant as described in Chapter 4. An understanding of these processes permits the development of a predictive simulation model describing eelgrass nutrient utilization (Chapter 6). Further, Chapter 3 of this study examines the relationship between sediment nitrogen and the morphology of eelgrass leaves and roots. In Chapter 5, the extent of plant-sediment interaction reveals the impact of eelgrass colonization on sediment nitrogen resources.

The combination of the nutritional and background data (Chapters 1-5) establishes the understanding necessary to construct a simulation model of nitrogen utilization and eelgrass growth. Armed with such a construct, various questions regarding eelgrass nutrition are addressed. For example: Where and when does nitrogen limit eelgrass growth, if at all? How does the interaction of available light and nitrogen influence eelgrass growth and biomass? And is it possible to predict

the effect of certain environmental perturbations on the eelgrass bed?  
The answers to these and other questions provide information needed to  
better understand the role of eelgrass in coastal temperate oceans.

## CHAPTER 2: PATTERNS OF EELGRASS STANDING STOCK AND RELATED NITROGEN RESOURCES

### INTRODUCTION

Eelgrass, *Zostera marina* L., in shallow coastal waters shows a distinct seasonal pattern over most of its geographic range. Temporal studies of eelgrass biomass demonstrate a similarity in the cycle of leaf and root-rhizome biomass in Japan (Aioi 1980), France (Jacobs 1979, Denmark (Sand-Jansen 1975), Rhode Island, USA (Brown 1962; Short 1975), Washington, USA (Phillips 1972), and Alaska, USA (McRoy 1966, 1974). An interactive combination of climatic factors (total radiation, photoperiod, temperature, etc.) has been shown sufficient to simulate the seasonal growth cycle in Rhode Island (Short 1980).

The importance of geographical differences in climate to the growth of eelgrass is often obscured by the local effects of physiographic factors (depth, turbidity, nutrients, etc.) which must also be considered. The depth at which the plants grow under natural conditions has been implicated as a factor controlling distribution (Short *et al.* 1974; Backman and Barilotti 1976). In addition, the available nutrient resources can affect both the eelgrass growth rate and the seasonal growth cycle (Orth 1977).

The patchiness in large eelgrass meadows confounds the study of standing stock in a seasonal and a spatial context. However, small areas of relatively uniform eelgrass standing stock characteristics (beds) are discernible within meadows. These eelgrass beds are distinct patches easily observed by an intensive sampling program (Short 1975).

Evidence for the magnitude of variation between eelgrass beds within a meadow is given in studies of seasonal biomass (McRoy 1966; Short 1975; Orth 1977). Local variation within an eelgrass meadow is attributable primarily to physiographic differences since climatic variations in a meadow are insignificant. As a result, the tidal depth, the attenuation of light due to depth, and the availability of sufficient nutrients for maximum growth appear to be the dominant environmental factors producing spatial differences in standing stock.

Light attenuation has received considerable attention and its impact on eelgrass growth and abundance is well documented (Burkholder and Doheney 1968; Short *et al.* 1974; Backman and Barilotti 1976; and Dennison 1979). The effect of diminished light with depth in coastal water is evidenced by decreased biomass and ultimate elimination of eelgrass.

The stimulation of eelgrass growth by addition of nutrient fertilizer to seawater has been evident for many years (Raymont 1947). More recently, enrichment of the sediment surface has demonstrated a quantitative increase in plant biomass within a few months (Orth 1977). These experiments suggested nutrient limitation in eelgrass beds but did not examine the naturally available nutrient resources. Studies of the availability and utilization of phosphate present no evidence of resource limitation but rather implicate eelgrass and other aquatic plants as a source of phosphate to the open water (McRoy and Barsdate 1970; McRoy *et al.* 1972; Barsdate *et al.* 1974; Carignan and Kalff 1979, 1980).

Open water sources of ammonium and nitrate are potentially important as a supply of nitrogen to eelgrass leaves. Nitrogen in coastal

water is influenced by tidal exchange with the surrounding ocean, freshwater runoff, incorporation into planktonic or benthic plant biomass, and regeneration by pelagic or benthic organisms. Uptake measurements of ammonium and nitrate by eelgrass leaves (Chapter 4) indicate that ammonium is the preferred nitrogen source.

The anoxic sediment nitrogen pool in eelgrass meadows is composed primarily of reduced nitrogen in the form of ammonium, originating from organic decomposition and animal excretion. Ammonium concentrations in most anoxic marine sediments increase to high levels as a result of microbial activity (primarily linked to sulfate reduction) and are balanced by diffusion and adsorption (Berner 1977). Diagenic models for calculating ammonium regeneration and equilibrium profiles of interstitial ammonium concentrations have been used in the stoichiometric analysis of organic degradation (Bender *et al.* 1977; Berner 1977; Vanderborght *et al.* 1977; Martens *et al.* 1978). Ammonium is removed from the sediment interstitial water by molecular diffusion upward into the water column (Krom and Berner 1980) and by adsorption onto the sediment surface. A chemical equilibrium has been observed in non-seagrass sediment between the ammonium in the interstitial water and the fraction of ammonium that can be removed by ion exchange from the sediment particles (Rosenfeld 1979; Blackburn 1979a).

The anoxic interstitial water in eelgrass meadows has an additional sink for ammonium: the plants. Eelgrass takes up ammonium and to some extent nitrate from the interstitial water through its roots, and transports nitrogen to the leaves for metabolic requirements (McRoy and Goering 1974; Iizumi 1979; Chapter 4). Nitrification at the eelgrass

root surface also reduces the ammonium interstitial concentration when oxygen leaks from the roots, although this effect is small relative to the ammonium pool size (Iizumi *et al.* 1980).

The availability of nitrogen resources to the spatial and temporal requirements for eelgrass growth is examined here in relation to observed eelgrass standing stock.

#### SITE AND METHODS

Eelgrass samples and sediment nutrient measurements were collected during the summers of 1976-79 in the vicinity of Grant Point in Izembek Lagoon (Fig. 2.1). Stations were selected to provide a variety of intertidal and subtidal eelgrass beds having different plant stocks and different sediment interstitial ammonium concentrations. The numbered station series was a transect established across a shallow tide pool and into deeper water away from shore. The other stations (Fig. 2.1) were selected for their distinctive sediment nutrient composition.

Plant samples were collected by clipping in a  $1/16 \text{ m}^2$  quadrant for leaves and by coring with a 16 cm diameter tube for roots and rhizomes. Shoot density was measured by counting fresh samples, and biomass was determined after drying to constant weight at 90°C for 24 hr.

Interstitial ammonium concentrations were determined from replicate 4.7 cm diameter cores manually collected from each station. The core samples were sectioned into a sediment squeezer (Reeburgh 1967) and the interstitial water was filtered through a glass fiber filter into a sealed "Vacutainer". Exchangeable ammonium was measured on fresh or frozen sediments using 2 ml of 2 N KCl per 4 g of sediment

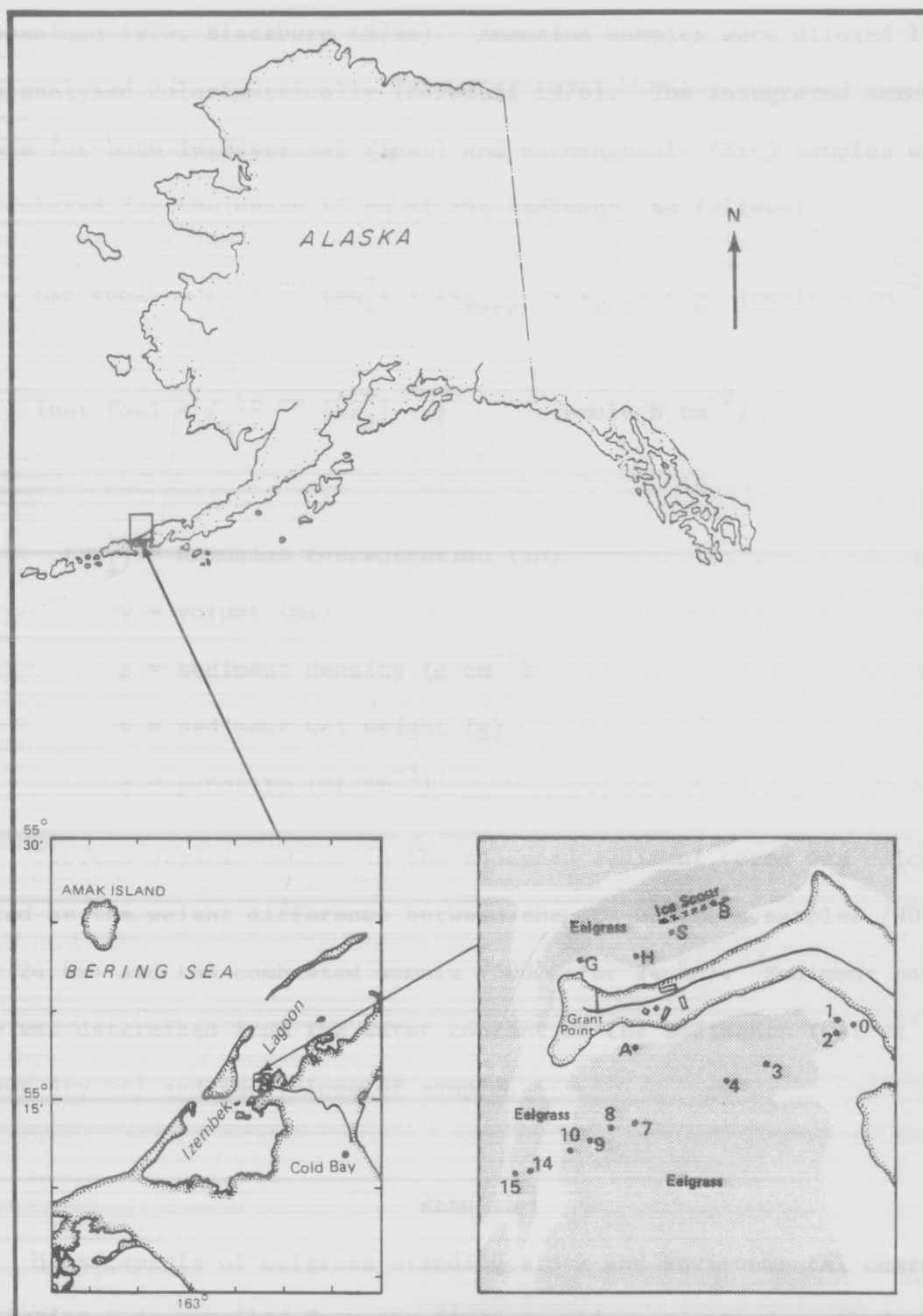


Figure 2.1. Map of Alaska showing locations of Izembek Lagoon and Grant Point. The area of continuous eelgrass meadow (shading), an ice scoured area, and the sampling stations are shown.



(Rosenfeld 1979; Blackburn 1979a). Ammonium samples were diluted 1:10 and analyzed colorimetrically (Koroleff 1976). The integrated ammonium pools for both interstitial (Inst) and exchangeable (Exc) samples were calculated for the upper 15 cm of the sediment, as follows:

$$\text{Exc Pool} = \int_0^{15 \text{ cm}} [\text{NH}_4^+] \cdot (V_{\text{Water}} + V_{\text{KCl}}) \cdot \frac{\rho}{w} \quad (\text{mmole N cm}^{-2})$$

$$\text{Inst Pool} = \int_0^{15 \text{ cm}} [\text{NH}_4^+] \cdot \phi \quad (\text{mmole N cm}^{-2})$$

where

$[\text{NH}_4^+]$  = ammonium concentration ( $\mu\text{M}$ )

$V$  = volume (ml)

$\rho$  = sediment density ( $\text{g cm}^{-3}$ )

$w$  = sediment wet weight (g)

$\phi$  = porosity ( $\text{ml cm}^{-3}$ )

Percent organic matter in the squeezed sediment cores was calculated as the weight difference between the dry sediment samples ( $90^\circ\text{C}$  for 24 hr) and the combusted sample ( $500^\circ\text{C}$  for 24 hr). Sediment porosity was determined from the water content of the sediments (wet wt minus dry wt) and the volume of sample.

## RESULTS

Measurements of eelgrass standing stock and environmental characteristics were compiled from the field sampling program described above and from other investigations at Izembek Lagoon (Dennison 1979; McRoy unpublished). The plant measurements and sediment characteristics

(Table 2.1) are used in a linear cross correlation analysis as an initial step in the investigation of the plant-sediment interaction. These results (Table 2.2) demonstrate a highly significant correlation ( $\alpha = 0.01$ ) between mean water depth and shoot density, leaf dry wt per shoot, porosity, organic content, and the interstitial ammonium pool. Significant correlations to shoot density and leaf length are also observed for sediment porosity, organic content, and interstitial ammonium.

The increase in eelgrass standing stock across the transect is accompanied by an increase in sediment organic content (Table 2.1). These data represent a spatial and depth average of the 0-5, 5-10, 10-15 cm of sediment for three replicate core samples. The mean and 95% C.I. for percent organic content for individual stations increases with distance from shore along the transect (Fig. 2.2).

The dynamics of the water column nitrogen cycle are not addressed in detail; water column data is assembled for ammonium and nitrate concentrations from data collected between 1969 and 1979 in Izembek Lagoon (Fig. 2.3a, b). Nitrate and ammonium show peak concentrations in winter and early spring and relatively low concentrations from May to November during the time of maximum eelgrass biomass. Concentrations of ammonium are higher than nitrate during the summer as a combined result of diffusion from the sediments, animal excretion, and high rates of organic decay. The daily variation in summer ammonium concentrations is a result of increases from local ammonium production and depletion from eelgrass and algal uptake. Spatial variation in ammonium concentrations is affected similarly; however, at each station the tidal

Table 2.1. Description of standing stock and environmental conditions for Izembek Lagoon, 1976-1979.\*

Date M-Y	Sta	WATER		EELGRASS					SEDIMENT		
		Temp Max °C	Water Depth (cm)	Shoot Density # m <sup>-2</sup>	Leaf Dry wt g shoot <sup>-1</sup>	Leaf Biomass g m <sup>-2</sup>	Root Biomass g m <sup>-2</sup>	Spadix # m <sup>-2</sup>	Porosity φ ml cm <sup>-3</sup>	Organic Content %	NH <sub>4</sub> <sup>+</sup> Pool**
7-76	A	22.0	60	10100	0.034	339	269	3005	0.68	3.65	2.99
7-76	H	16.5	120	3800	0.151	575	387	3335	0.77	3.71	15.10
6-76	B	18.0	100	1888	0.125	236	533	576	0.65	5.30	11.18
6-76	S	18.0	100	3552	0.073	261	339	0	0.83	7.05	20.27
6-76	G	18.0	120	2016	0.176	355	343	0	0.82	6.48	49.10
7-77	2	15.7	30	3300	0.044	146	282	1520	0.71	5.43	4.50
7-77	4	15.0	30	5034	0.078	394	527	2205	0.54	2.82	3.87
7-77	7	15.1	50	3500	0.107	373	575	2125	0.69	5.66	5.12
7-77	10	14.7	90	1700	0.378	643	722	245	0.83	7.85	25.94
7-77	15	14.7	130	685	0.391	268	719	48	0.84	11.04	94.79
6-78	1	20.0	30	6562	0.021	79	195	221	0.66	3.12	2.33
6-78	2	20.0	30	10203	0.025	185	532	1771	0.73	3.91	1.58
6-78	4	20.0	30	9308	0.021	154	1612	984	0.50	3.15	0.97
6-78	8	19.5	70	5393	0.056	301	588	228	0.69	5.55	2.49
6-78	9	21.0	80	2570	0.090	231	834	166	0.68	6.55	8.53
6-78	14	20.0	100	1249	0.122	202	849	0	0.78	5.76	58.18
8-79	2	15.9	30	8336	0.030	254	562	320	0.59	2.80	2.63
8-79	8	16.3	60	3520	0.136	479	290	483	0.73	6.03	3.35

\*Data from McRoy and Klug (unpublished); this study.

\*\*Integrated ammonium pool 0-15 cm in sediment,  $\int_0^{15}$  mmole N m<sup>-2</sup>.

Table 2.2. Correlation matrix for eelgrass and environmental data from Table 2.1.  
(99% significance level underlined).

Water Depth*	Shoot Density	Leaf Dry Wt	Leaf Biomass	Root Biomass	Spadix #	Porosity $\phi$	% Organic	NH <sub>4</sub> <sup>+</sup> Pool	
-0.12	0.46	-0.55	-0.50	0.15	-0.03	-0.18	-0.33	-0.23	Temp Max
	<u>-0.71</u>	<u>0.68</u>	0.38	-0.06	-0.24	<u>0.74</u>	<u>0.68</u>	<u>0.73</u>	Water Depth
		<u>-0.68</u>	-0.30	0.09	0.41	<u>-0.59</u>	<u>-0.73</u>	<u>-0.60</u>	Shoot Density
			0.56	0.08	-0.27	<u>0.63</u>	<u>0.80</u>	<u>0.73</u>	Leaf Dry Wt
				-0.16	0.29	0.34	0.19	0.06	Leaf Biomass
					-0.19	-0.37	0.03	0.12	Root Biomass
						-0.26	-0.50	-0.39	Spadix #
							<u>0.74</u>	<u>0.64</u>	$\phi$ , Porosity
								<u>0.75</u>	% Organic

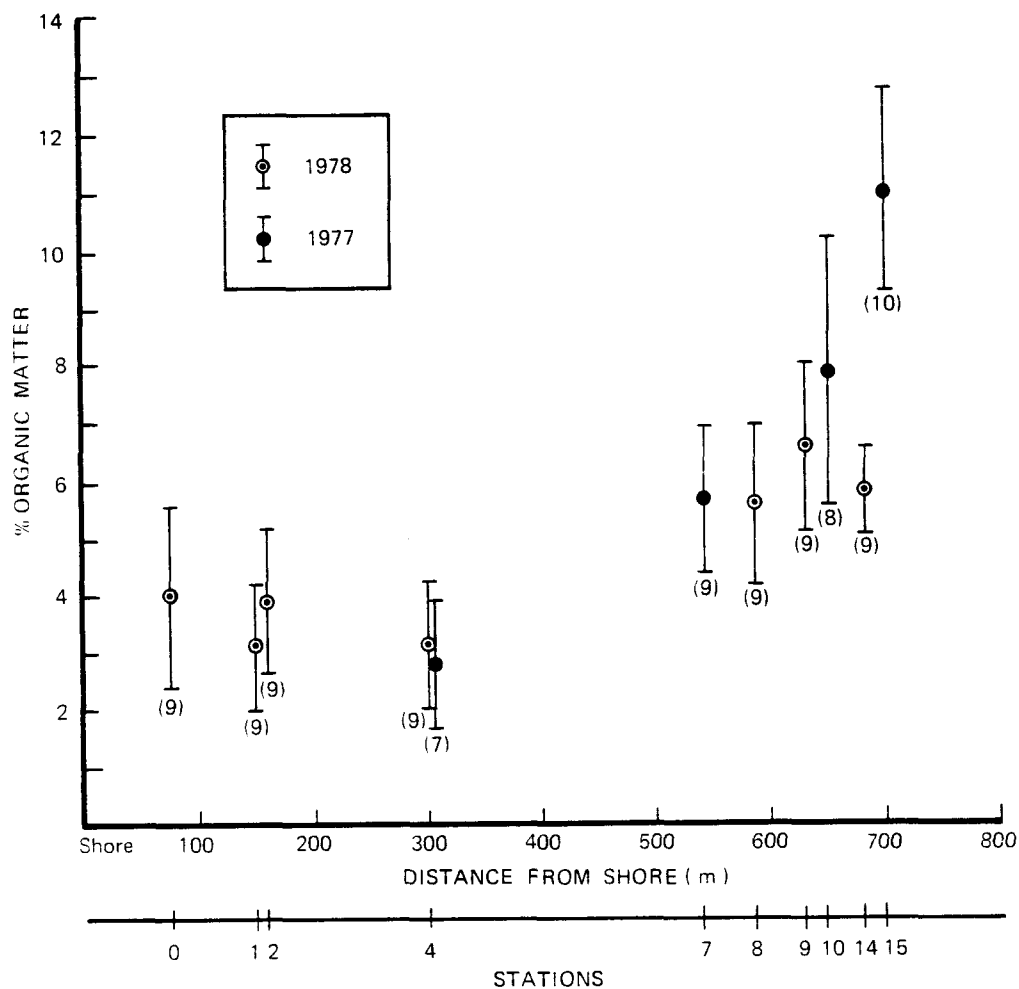


Figure 2.2. Sediment organic content vs. distance from shore and station numbers along the transect. Mean and 95% C.I. of percent organic content for 1977 and 1978. Number of samples is given in parentheses (Data from McRoy and Klug unpublished).

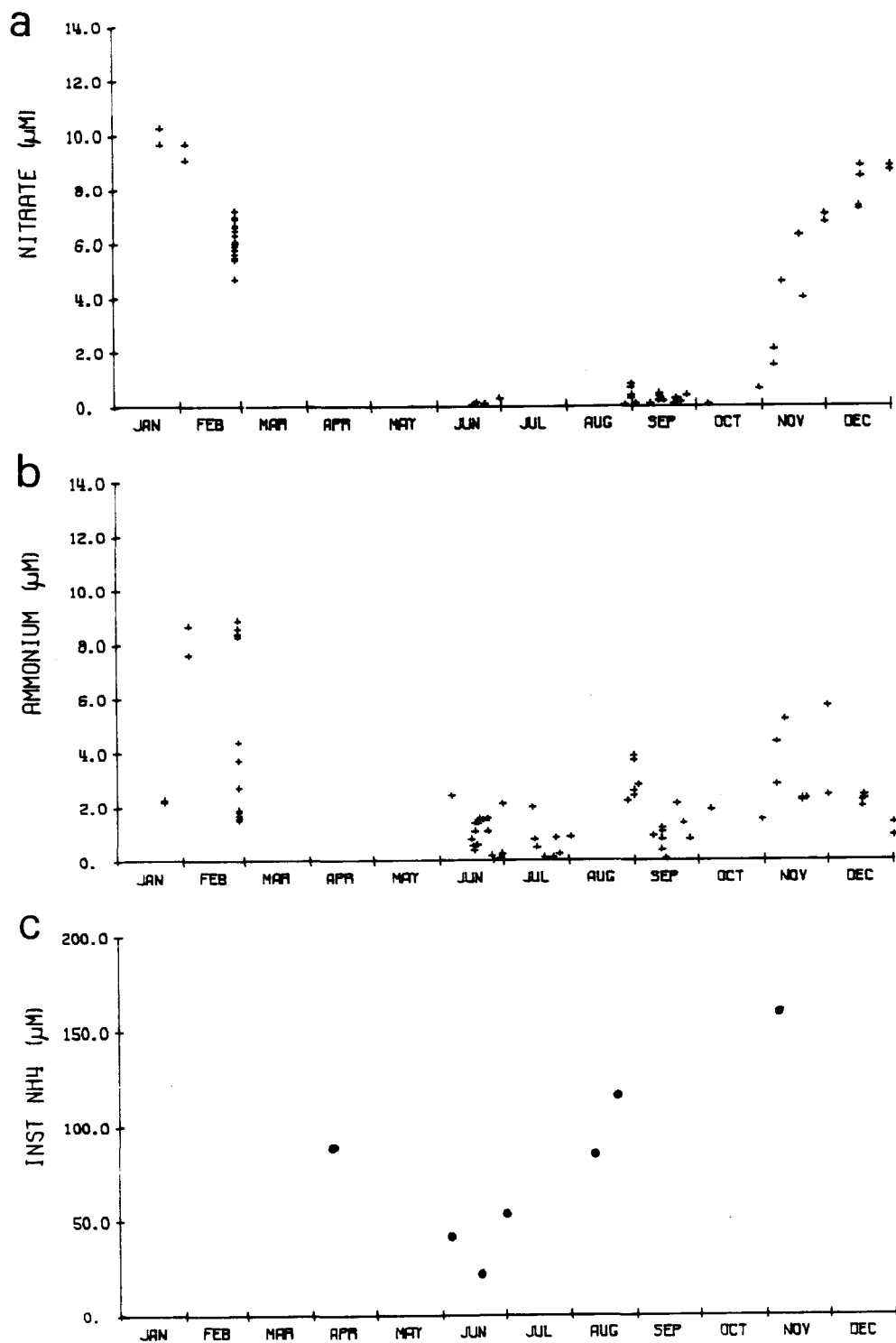


Figure 2.3. Nitrate (a) and ammonium (b) concentration in the water column in Izembek Lagoon, 1969-1979. (Data from McRoy *et al.* 1972b; McRoy unpublished; this study). Ammonium (c) concentration in the interstitial water (INST NH<sub>4</sub>) at Station S, 1976-79; individual samples of average ammonium concentration over the upper 15 cm of sediment.

exchange continually exposes the eelgrass plants to low but varying nitrogen concentrations.

Nitrogen in eelgrass sediments at Station S in Izembek Lagoon demonstrates a seasonal cycle in interstitial ammonium concentrations depicted by a sharp drop in the spring to a low point in summer and an increase in early fall through winter (Fig. 2.3c). This pattern is also evident at all the transect stations except Station 1 where high ammonium concentrations were found on 31 July 1978 (Table 2.3). Concentrations of interstitial ammonium range from 3 to 2000  $\mu\text{M}$  across the eelgrass meadow; however, profiles of ammonium within smaller eelgrass beds are relatively uniform in shape and magnitude (Fig. 2.4). These profiles show low ammonium levels in the upper 10 cm of sediment, generally increasing concentrations from 10-20 cm, and a nearly constant concentration down to 25 cm.

The pools of interstitial and adsorbed (exchangeable) ammonium in eelgrass sediments are correlated to organic content during mid-July; in August however the relationship is less obvious (Table 2.4). Ratios of exchangeable to interstitial ammonium showed a decrease from the low organic to the high organic sediments in July, while in August the ratios were relatively constant (Table 2.4).

## DISCUSSION

The availability of nitrogen to a coastal lagoon ecosystem was examined in relation to eelgrass standing stock. The sources of nitrogen required for eelgrass growth are ammonium and nitrate from the water column and ammonium in anoxic sediments (Fig. 2.5a). A generalized

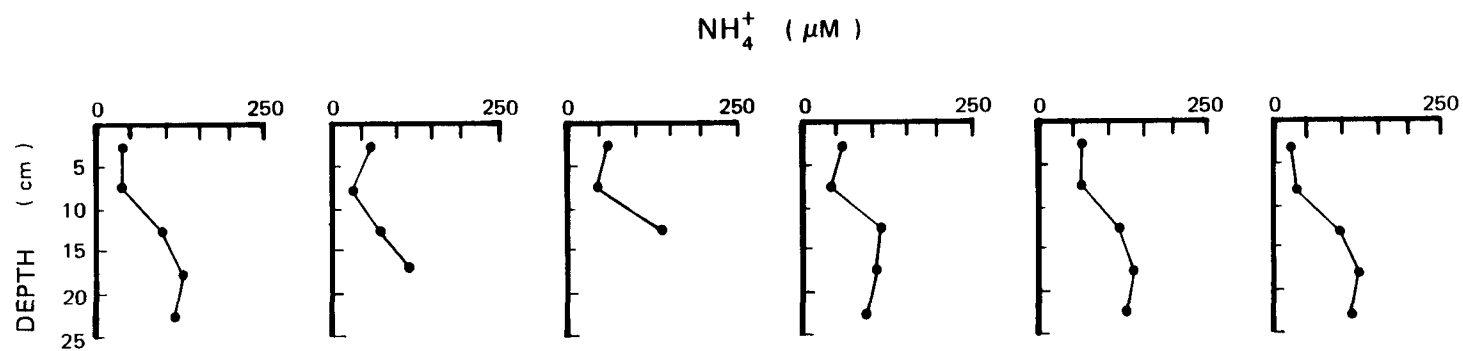


Figure 2.4. Profiles of interstitial ammonium concentration vs. depth in the sediments at Station S, Izembek Lagoon. Six replicate cores collected within one square meter on 30 June 1976. The average variance between cores for the upper 25 cm is 20% of the mean.



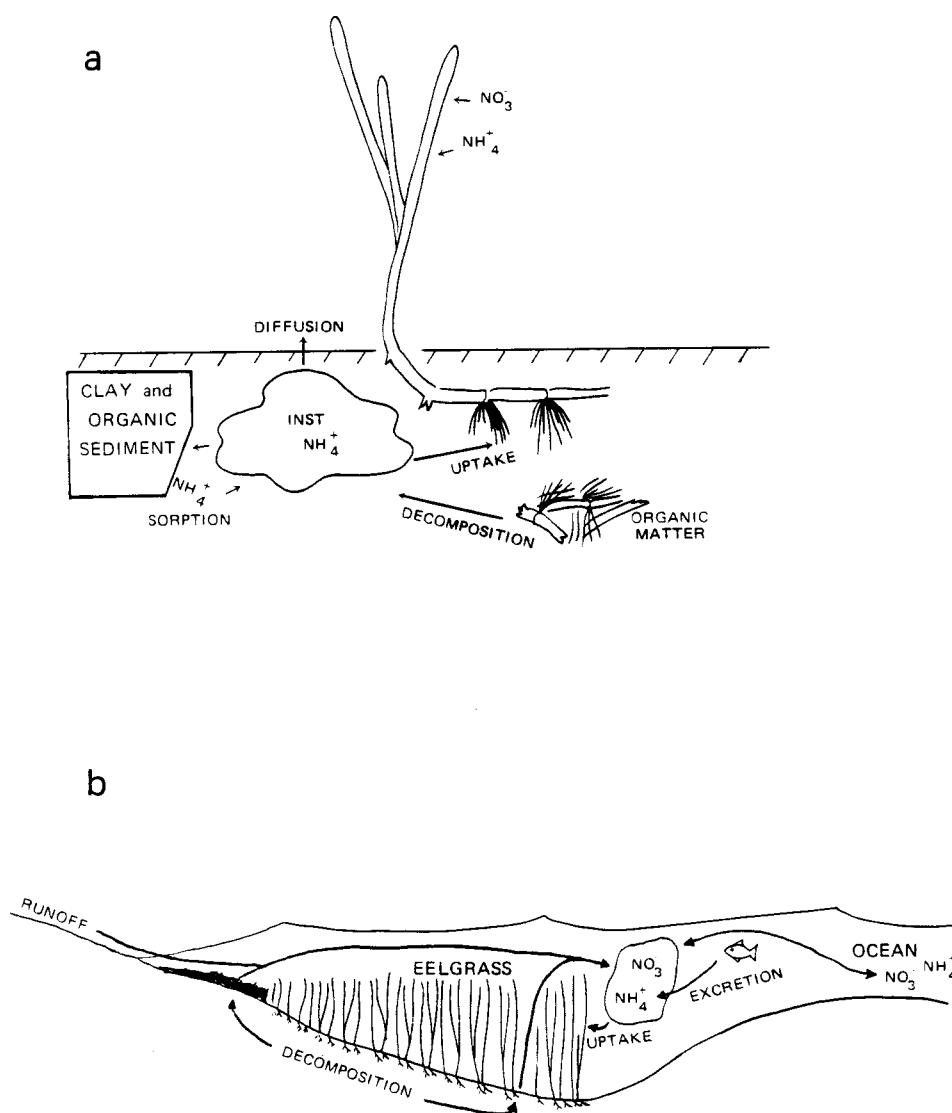


Figure 2.5. Illustration of the major components of the cycles of ammonium and nitrate in an eelgrass bed (a) and Izembek Lagoon (b).

Table 2.3. Average interstitial  $\text{NH}_4^+$  concentration ( $\mu\text{M}$ ) in the upper 19 cm of eelgrass sediment of each station, 1978\*.

Station	18 June	31 July	20 August
1	39.5	78.0	18.1
2	96.3	71.0	99.4
4	463.3	178.0	252.0
8	478.2	44.5	212.7
9	725.0	173.8	196.1
14	870.8	500.7	464.4

\*Data collected with diffusion equilibrators by McRoy and Klug (unpublished).

Table 2.4. Interstitial and exchangeable ammonium in the upper 15 cm of eelgrass sediments (mean  $\pm$  95% C.I., n = number of samples).

Date	Sta	% Organic Content	Inst* $\text{NH}_4^+$ n=3	Exc** $\text{NH}_4^+$ n=4	Ratio Exc:Inst
mid-July 1977	4	2.8	3.9 (0.5)	56.0 (3.2)	14.4
	7	5.7	5.1 (1.5)	59.7 (5.9)	11.7
	10	7.8	25.9 (9.6)	48.0 (12.9)	1.9
	14	7.9	57.2	90.3	1.6
	15	11.0	94.8 (15.9)	95.6 (43.0)	1.0
			n=4	n=1	
mid-August 1979	2	2.8	2.6 (0.5)	14.3	5.5
	3	3.9	3.0 (0.6)	13.7	4.7
	9	4.6	3.2 (0.8)	10.1	3.2
	8	6.0	3.3 (0.3)	12.5	3.8
	7	7.6	3.3 (1.1)	14.5	4.5

\*Inst  $\text{NH}_4^+$  is the interstitial water ammonium pool,  $\int_0^{15\text{cm}}$  mmole N  $\text{m}^{-2}$ .

\*\*Exc  $\text{NH}_4^+$  is the KCl exchangeable ammonium,  $\int_0^{15\text{cm}}$  mmole N  $\text{m}^{-2}$ .

nitrogen cycle for this ecosystem includes contributions from tides, streams, animal excretion, and organic decomposition balanced by removal through tidal flushing, uptake by benthic and pelagic plants, and export of drifting plant material (Fig. 2.5b).

A wide range of variation in eelgrass standing stock is evident for the eelgrass seasonal cycle in Izembek Lagoon, although this area has uniform climatological conditions. Thus, the differences in leaf dry weight per shoot across this eelgrass meadow (Fig. 2.6) can be attributed to environmental variations within the meadow. Significant correlation of both leaf dry weight and shoot density with sediment ammonium and organic content suggests the importance of substrate to eelgrass growth (Table 2.2). Similarly, the aboveground biomass of two salt marsh macrophytes significantly correlated with interstitial ammonium concentrations (Smart and Barko 1980).

Nitrogen in the sediments is directly available to the plants through the root and rhizome system. Ammonium is the dominant form of nitrogen in these anoxic sediments although low nitrate concentrations were reported in association with oxygen released by eelgrass roots (Iizumi *et al.* 1980). These nitrate concentrations (0-9.8  $\mu\text{M}$ ) are fifty to one hundred times less than those reported for ammonium at the same stations. In other studies, nitrogen fixation was found to be an important source of nitrogen to tropical seagrasses (Capone *et al.* 1979); but in temperate seagrass ecosystems with typically organic-rich sediments,  $\text{N}_2$  fixation was not found to be an important part of the plant nitrogen resource (Lipschultz *et al.* 1979; McRoy and McMillan 1977).

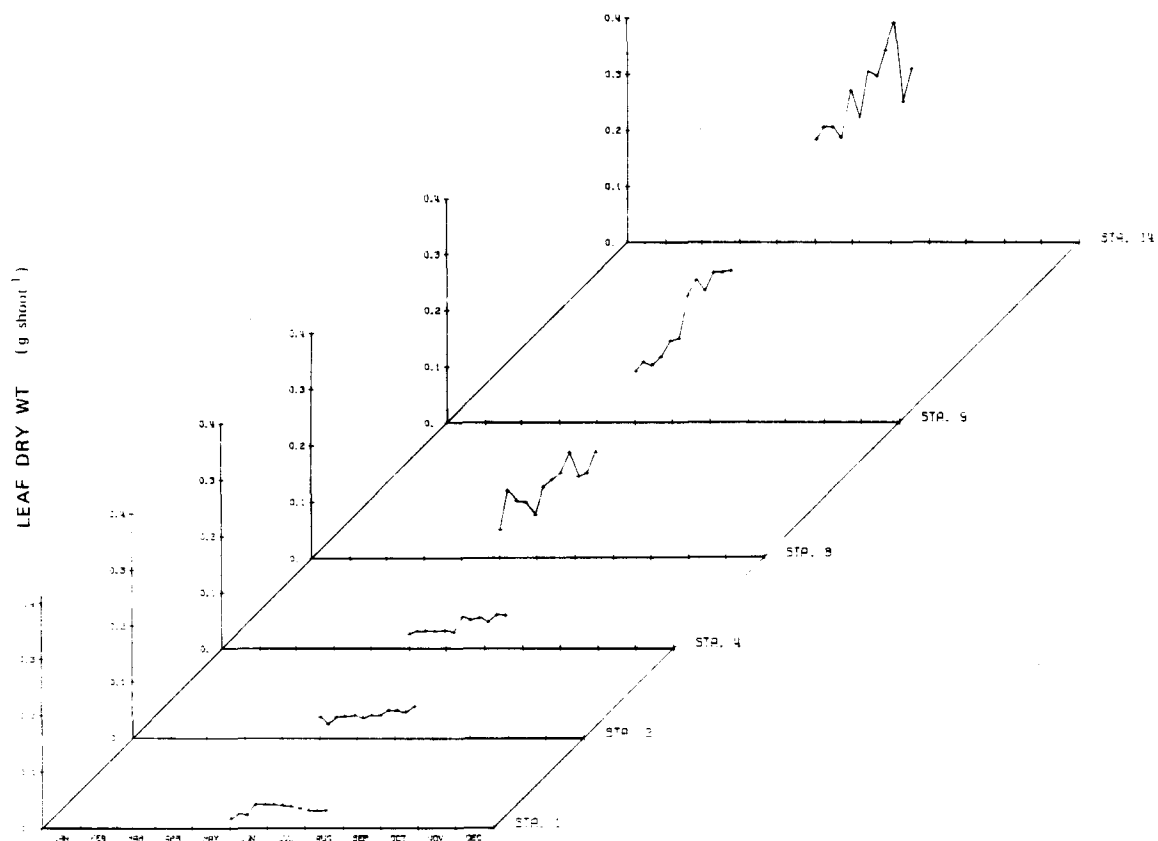


Figure 2.6. Eelgrass leaf dry weight per shoot during the summer of 1978. Mean of ten plants collected weekly at six stations along the transect (Data from Dennison 1979).

Profiles of ammonium concentrations with depth in Izembek Lagoon (Fig. 2.4) indicate reduced concentrations in the upper 15 cm relative to profiles of ammonium in non-seagrass sediments from other locations (Grundmanis and Murray 1977; Murray *et al.* 1978; Rosenfeld 1979; Blackburn 1979a, b; McCaffrey *et al.* 1980). Ammonium-depth profiles from tropical seagrass beds also indicate ammonium depletion in the root zone (Patriquin 1972).

The pool of interstitial ammonium in the Izembek eelgrass sediments is significantly correlated with the organic content in the sediments (Table 2.2). This relationship results from the production and buildup of ammonium in the process of anoxic decomposition of organic matter, and is demonstrated by the increase of ammonium and organic matter as one moves from the intertidal to the subtidal. The decomposition rate for eelgrass leaves has been examined (Harrison and Mann 1975) but contributions to sediment decomposition from release of dissolved organic material and by root-rhizome death remain to be studied. Knowledge of the chemical composition of these organic components would permit calculations of the ammonium production rate based on the stoichiometric decay rates (Berner 1977; Aller and Yingst 1980).

Three major losses of ammonium from the interstitial ammonium pool in eelgrass sediments deserve examination: diffusive flux across the sediment-water interface, ion exchange at the surface of clay and organic matter, and uptake by eelgrass roots (Chapter 4). Diffusive flux has been described for a number of different marine sediment environments (Hale 1976; McCaffrey *et al.* 1980; Martens *et al.* 1980; Krom and

Berner 1980). These diffusion rates are in the same range as those found in eelgrass sediments (Chapter 5).

Ammonium ion exchange between the interstitial water and clay or organic material has been measured in several marine environments (Patriquin 1972; Rosenfeld 1979; Blackburn 1979a, b). These authors found an equilibrium between the exchangeable (Exc) ammonium adsorbed onto the sediment and the interstitial (Inst) ammonium. The non-seagrass sediment demonstrated an Exc:Inst ratio between 1:1 and 2:1 (Rosenfeld, 1979; Blackburn, 1979a, b). However, sediments of the tropical seagrass *Thalassia testudinum* had an equilibrium ratio of 64:1 (Patriquin, 1972). The ratio of exchangeable to interstitial ammonium in eelgrass beds varied from a ratio of 1:1 to 14:1 across the Izembek transect. This ratio is negatively correlated to the organic content in the sediment, with the largest ratio at the stations with lowest organic content (Table 2.4). Thus in July the stations with low organic sediment, low interstitial ammonium, and little exchangeable ammonium displayed a very steep gradient from adsorbed to interstitial ammonium. This gradient is maintained at these stations by the high rate of ammonium uptake by eelgrass roots relative to the size of the ammonium pool. At stations with high organic content, a large interstitial ammonium pool, and a Exc:Inst ratio in the low range ( $\sim$ 1:1), the effect of eelgrass uptake on the equilibrium is not evident. However by mid-August, the exchangeable ammonium is depleted to low levels at all these stations and the ratio indicates a relatively steep gradient ( $>3:1$ ) between adsorbed and interstitial ammonium.

This implies active depletion of the sediment ammonium pool at many stations across the transect.

The seasonal cycle of ammonium in the interstitial water of an eelgrass bed demonstrates the depletion of ammonium in mid-summer (Fig. 2.3c and Table 2.3) at the time of maximum leaf biomass (Fig. 2.6). However, the pattern of seasonal ammonium production in non-seagrass sediments indicates a summer maximum and a strong correlation with temperature (Blackburn 1979b), suggesting a peak in the sediment ammonium pool should occur in mid-summer in Izembek Lagoon. Further evidence suggesting a summer ammonium maximum in marine sediments is provided by the high rates of diffusive flux observed during the summer months and very low rates in winter (Nixon *et al.* 1976; Martens *et al.* 1980). Ammonium flux from the sediment surface, which is driven by concentration, also shows a significant exponential relationship with temperature (Nixon *et al.* 1976). The seasonal pattern in ammonium production, concentration driven diffusion, and a limited ammonium ion exchange capacity in the sediments again all suggest that the additional sink for ammonium in eelgrass sediments is uptake by the plant roots.

#### CONCLUSIONS

The standing stock of eelgrass in both a spatial and temporal context correlates with the availability of ammonium in the eelgrass sediments, implying the importance of this resource as a major environmental control of eelgrass growth. Sediment ammonium is the largest source of nitrogen available to eelgrass growth. The utilization of this resource



is evidenced by the concentration depletion in both the interstitial profiles and the seasonal ammonium pool size in eelgrass sediments. Examination of ammonium production and the extractable ammonium pool suggests that uptake by eelgrass roots in July more than compensates for the ammonium renewal from decomposition and ion exchange at many stations. Nitrogen is also available from the water column in the form of nitrate and ammonium; however, during most of the growing season the water column concentrations are very low.

The occurrence of eelgrass beds with low standing stock and small sediment ammonium reserves suggests that in organic-poor sediments the available nitrogen supply could limit eelgrass growth. Areas of organic-rich sediment having large ammonium reserves may also experience periods of insufficient nitrogen for plant metabolism when the rate of supply does not equal the plant uptake rate. Thus, across the expanse of an eelgrass meadow the degree to which nitrogen limits eelgrass growth could vary from little to no effect during the peak summer growth to depleted nitrogen resources year round.

### CHAPTER 3: THE MORPHOLOGY OF EELGRASS, *ZOSTERA MARINA* L. IN RELATION TO SEDIMENT AMMONIUM IN IZEMBEEK LAGOON, ALASKA

#### INTRODUCTION

The striking difference in eelgrass morphology between areas of different substrate was described early in the study of these perennial marine macrophytes (Ostenfeld 1908). So obvious was the relation between the plant morphology and the sediment environment that Ostenfeld described two forms, both growing in deep water, as the "narrow-leaved sand *Zostera*" and the "broad-leaved mud *Zostera*". Some time later Philip (1936) described this same phenomenon as the inshore narrow-leaved and the offshore broad-leaved forms of *Zostera marina* occurring in different substrates. Additionally, in his analysis of chemical factors limiting *Zostera* distribution Philip suggested that "the nitrogen content of the mud" might account for the differences in leaf size.

Numerous other investigations have described different growth forms of *Zostera marina* and related them to variations in several environmental factors (temperature, Setchell 1929 and McRoy 1966; light, Burkholder and Doheny 1968; wave action and substrate, Harrison and Mann 1975; sediment texture, Aioi 1980). However, the only study that has expanded on the implications of Philip's 1936 suggestion that nutritional factors might be important in controlling eelgrass morphology is a fertilizer enrichment experiment by Orth in 1977.

My study describes the influence of various environmental factors on the size of eelgrass plants and the structure of eelgrass beds. The eelgrass sediment environment is an anoxic system with an extensive

composition of chemical species (eg.  $\text{NH}_4^+$ ,  $\text{PO}_4^{-3}$ ,  $\text{H}_2\text{S}$ ,  $\text{CH}_4$ ,  $\text{H}^+$ ; McRoy and Klug unpublished) that could exert an influence on eelgrass morphology. Of these, ammonium ( $\text{NH}_4^+$ ) is a major nitrogen supply to the plants (Chapter 4) and shows large differences among eelgrass beds. The relation of sediment ammonium and various climatic factors to plant morphology is discussed, although the impact of ammonium on morphology cannot be separated from other chemical influences. The analysis is based on experimental and descriptive survey studies of the eelgrass ecosystem and a comparison with the literature on agricultural crop species.

#### METHODS

This assessment of the relationship between nitrogen supply and eelgrass morphology is approached using a simple comparison of resource availability and plant characteristics. Measurements of leaf length, width, and area along with shoot and flower density were made on a routine basis when sampling eelgrass standing stock in the vicinity of Grant Point in Izembek Lagoon (Fig. 2.1). Rhizome length data and observations of root structure were obtained from many of the same stations for comparison to above-ground data. Samples used in this analysis were collected during June and July from 1976 through 1978. Leaf material was clipped at the sediment surface within a  $1/16 \text{ m}^2$  quadrant and the plant material below the sediment surface was collected with a 16 cm diameter core sampler to a depth of about 30 cm from selected stations at Izembek Lagoon (Fig. 2.1). The values for leaf length and width were obtained by averaging the maximum leaf size of 10 vegetative

shoots. Leaf area was measured on the same shoots using a Lambda LI-3100 area meter. Eelgrass flowers (spadices) were removed from the reproductive stem and counted separately. Rhizome length was determined by adding the length of all rhizome segments collected in each core sample. Root size was observed on samples from several stations on the transect and root hair development was examined with a microscope.

The major nitrogen resource immediately available to the eelgrass plants is present in the root zone of an eelgrass bed. The size of the interstitial ammonium pool provides a good indicator of this resource (Chapter 2). Interstitial ammonium concentrations were determined from replicate core samples manually collected at each station. These core samples were sectioned into a sediment squeezer (Reeburgh 1967) and the interstitial water was filtered through a glass fiber filter into a sealed "Vacutainer". Ammonium samples were diluted 1:10 and analyzed colorimetrically (Koroleff 1976). The interstitial ammonium pool was calculated by integrating the observed ammonium concentrations, multiplied by the sediment porosity, over the upper 15 cm of the sediment and converting to area ( $m^2$ ).

## RESULTS

The morphology of eelgrass leaves and roots is graphically compared to the amount of available ammonium in the surface sediments of the root zone. Eelgrass shoots vary in size from small narrow-leaved plants in the nitrogen-poor sandy sediments to long wide-leaved plants in the nitrogen-rich muddy eelgrass beds.

### Leaf Size

The analysis of eelgrass leaves on a per shoot basis demonstrates good correlation between the ammonium pool and all leaf measurements (Fig. 3.1). These data show an increase in leaf area, leaf length, and leaf width with an increase in the ammonium pool up to about 15 mmole  $N\ m^{-2}$  (low nitrogen region); above this level (high nitrogen region) leaf size is relatively constant.

The size of eelgrass leaves growing at different nitrogen levels shows a response similar to that found in crop plants: "higher nitrogen supplies lead to larger leaves" (Milthorpe and Moorby 1974). However, the relationship between nitrogen supply and eelgrass leaf size is complicated by observed changes in water depth.

The low-nitrogen eelgrass beds are located on a shallow, gradually sloping terrace (tidepool) where all the plants have similar exposure at low tide and similar light regimes. Eelgrass in the nitrogen-rich beds is exposed to varying environmental conditions including water depth and light availability. The small differences in maximum water temperature during June and July ( $\approx 1.5^{\circ}C$ , Table 2.1) across the eelgrass meadow in Izembek Lagoon do not substantially affect eelgrass plant size.

### Shoot Density

Eelgrass shoot density demonstrates a statistically significant ( $\alpha = 0.01$ ) negative logarithmic correlation ( $R = 0.97$ ) with the interstitial ammonium pool size for all the eelgrass beds sampled (Fig. 3.2a). However, environmental factors other than sediment nitrogen must be considered as influences on shoot density. Light is the most obvious

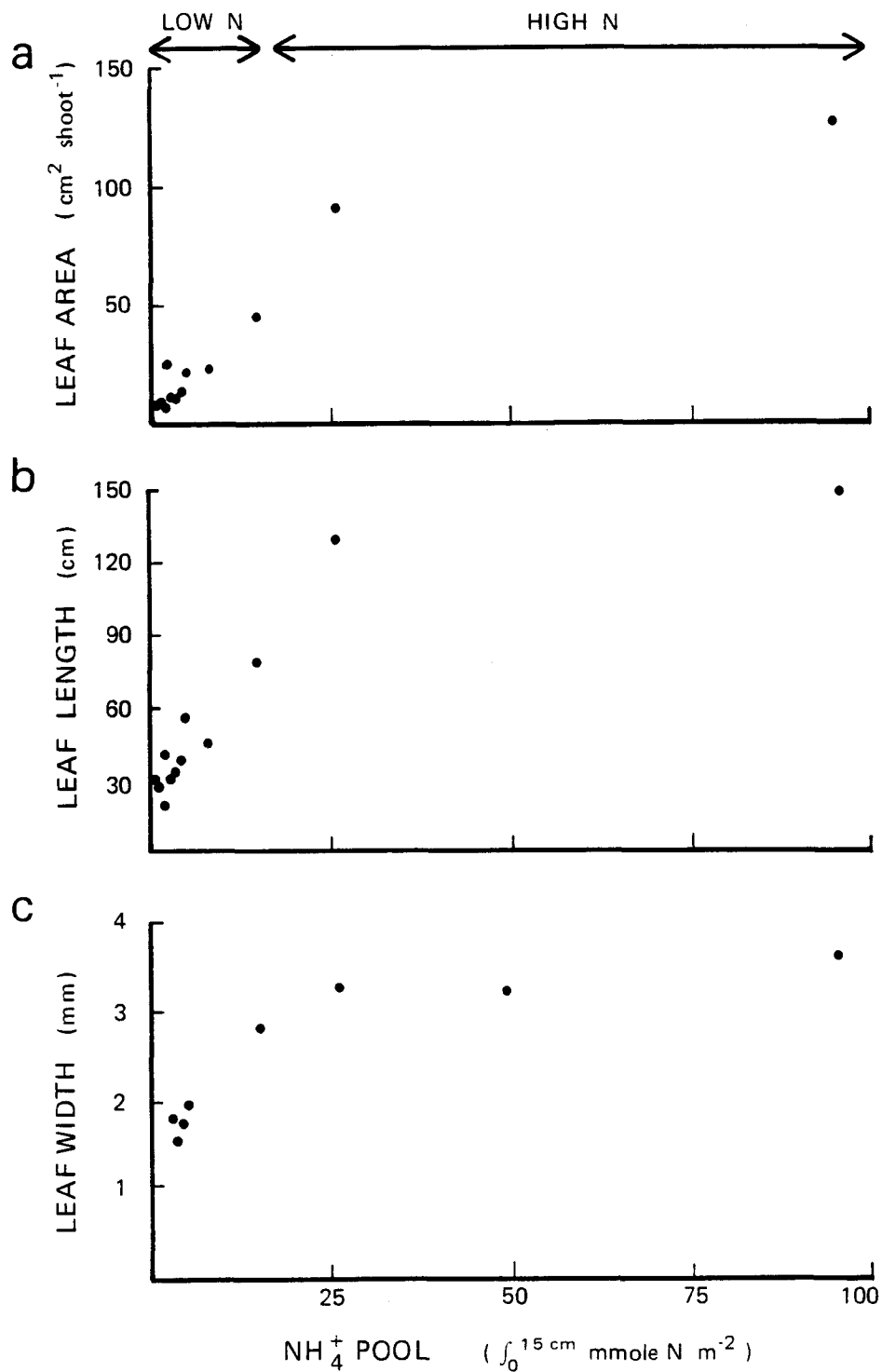


Figure 3.1. Relationship between eelgrass leaf size and the sediment interstitial ammonium pool for June 1976-78 (10 replicate shoots): (a) Mean leaf area per shoot; (b) Length of mature leaves; (c) Maximum leaf width (Data from Dennison 1979 and this study).

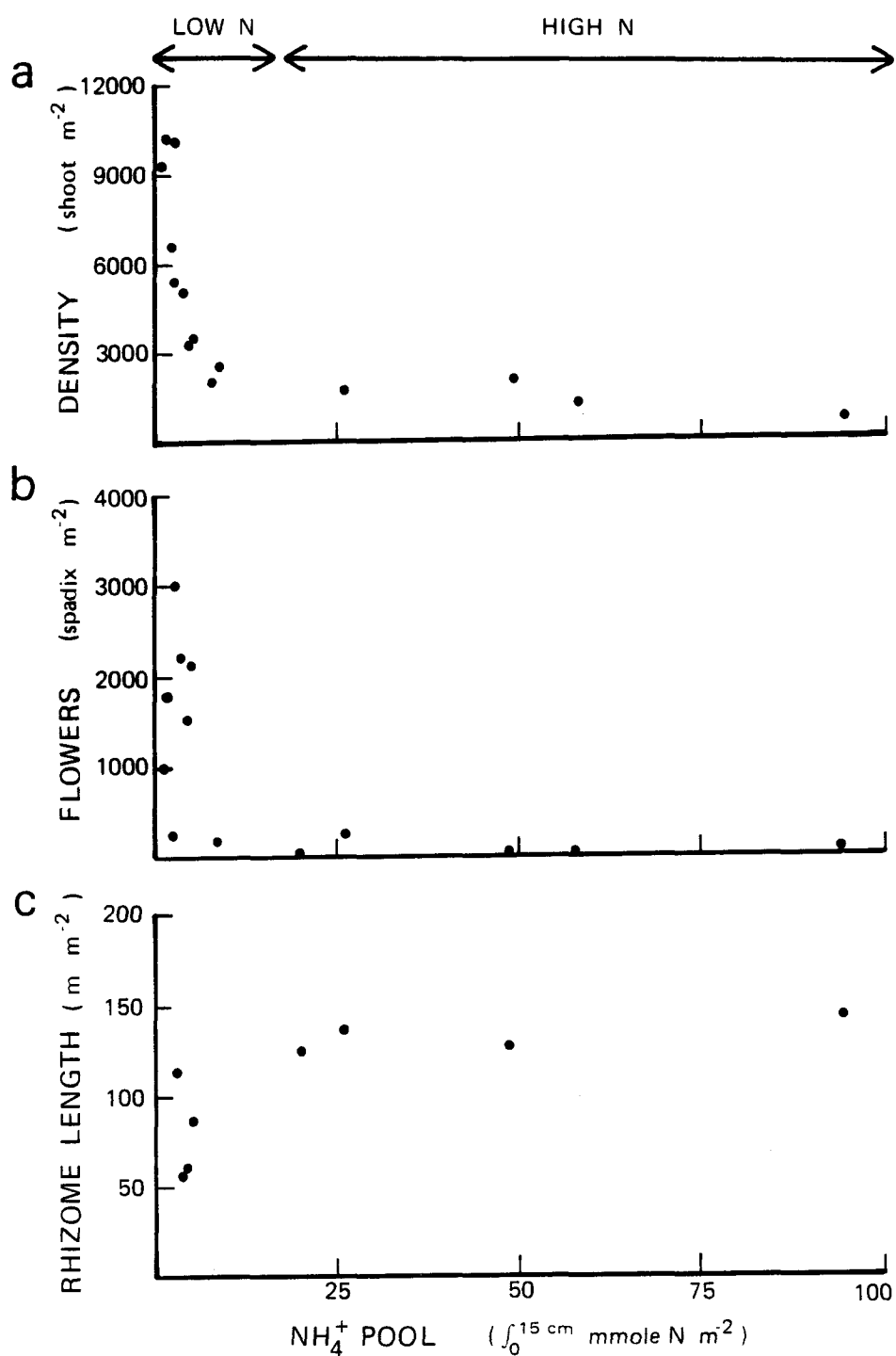


Figure 3.2. Relationship between eelgrass morphology and sediment interstitial ammonium pool for June and July 1976-78 (mean of replicate samples): (a) Shoot density  $\text{m}^{-2}$ , a statistical correlation of log transformed data is significant ( $R = 0.97$ ); (b) Flowering spadix density  $\text{m}^{-2}$ ; (c) Length of rhizome  $\text{m}^{-2}$ .

factor to be considered in regard to shoot density, since numerous studies have noted that both light and shoot density decrease with depth from the low tide level to some depth determined by the clarity of the water (Burkholder and Doheny 1968; Phillips 1972; Backman and Barilotti 1976; Jacobs 1979). Experimental evidence is available showing a decrease in shoot density with reduced light resulting from light attenuation with depth or from shading of plants at constant depth (Short *et al.* 1974; Backman and Barilotti 1976). The relationship between shoot density and light intensity is confirmed by extensive work with agricultural crop plants, in which reduced light decreases new shoot (tiller) production (Evans *et al.* 1964; Milthorpe and Moorby 1974).

The variation in light reaching shallow-water plants is small and its influence on shoot density is questionable. Keller and Harris (1966) found that shoot (turion) density did not vary over a depth range of about 1 m, but leaf size and biomass did change significantly.

### Flowering

Flowering in eelgrass beds reflects the same pattern as shoot density (Fig. 3.2b), with the largest number of flowering spadices in areas of very low sediment ammonium. The absence of flowers in the nitrogen-rich sediments was evident for all samples collected at Izembek Lagoon.

### Root and Rhizome

Eelgrass rhizome length per square meter of bottom, representing the size of the underground eelgrass system, shows a hyperbolic increase



in beds of increasing sediment ammonium (Fig. 3.2c). The size of the root and rhizome structure is directly associated with the leaf size for all stations. A large variation in root structure (Fig. 3.3) was observed at Izembek Lagoon, with large-diameter long roots and reduced root hairs in the nitrogen-rich muds, and shorter fine roots and abundant root hairs in the nitrogen-poor sandy sediments. This wide range of root and root hair size was not observed in previous eelgrass studies (Smith *et al.* 1979). The root structure in the low-nitrogen environment consists of 2 bundles of 10 fine roots extending vertically 10-15 cm into the sediment from each rhizome node. Each root is covered with dense root hairs similar to those described by Smith *et al.* (1979) providing a large rhizosphere. The development of root hairs, although not quantitatively examined, appeared related to the sediment nitrogen pool. The greatest extreme existed between the root system in the low-nitrogen environment and the root systems in the nitrogen-rich sediment (Fig. 3.3). Short root hairs were observed on the coarse white roots that extended far into the sediment in the nitrogen-rich soft mud, while in the sandy nitrogen-poor sediment the shorter roots were covered with rusty-brown root hairs (the color appeared to result from oxidation of iron on the root hair surface).

## DISCUSSION

The gross morphological differences between eelgrass plants within a single eelgrass meadow have been described in a number of studies (Sand-Jenson 1975; Short 1975; Jacobs 1979; Aioi 1980). These studies

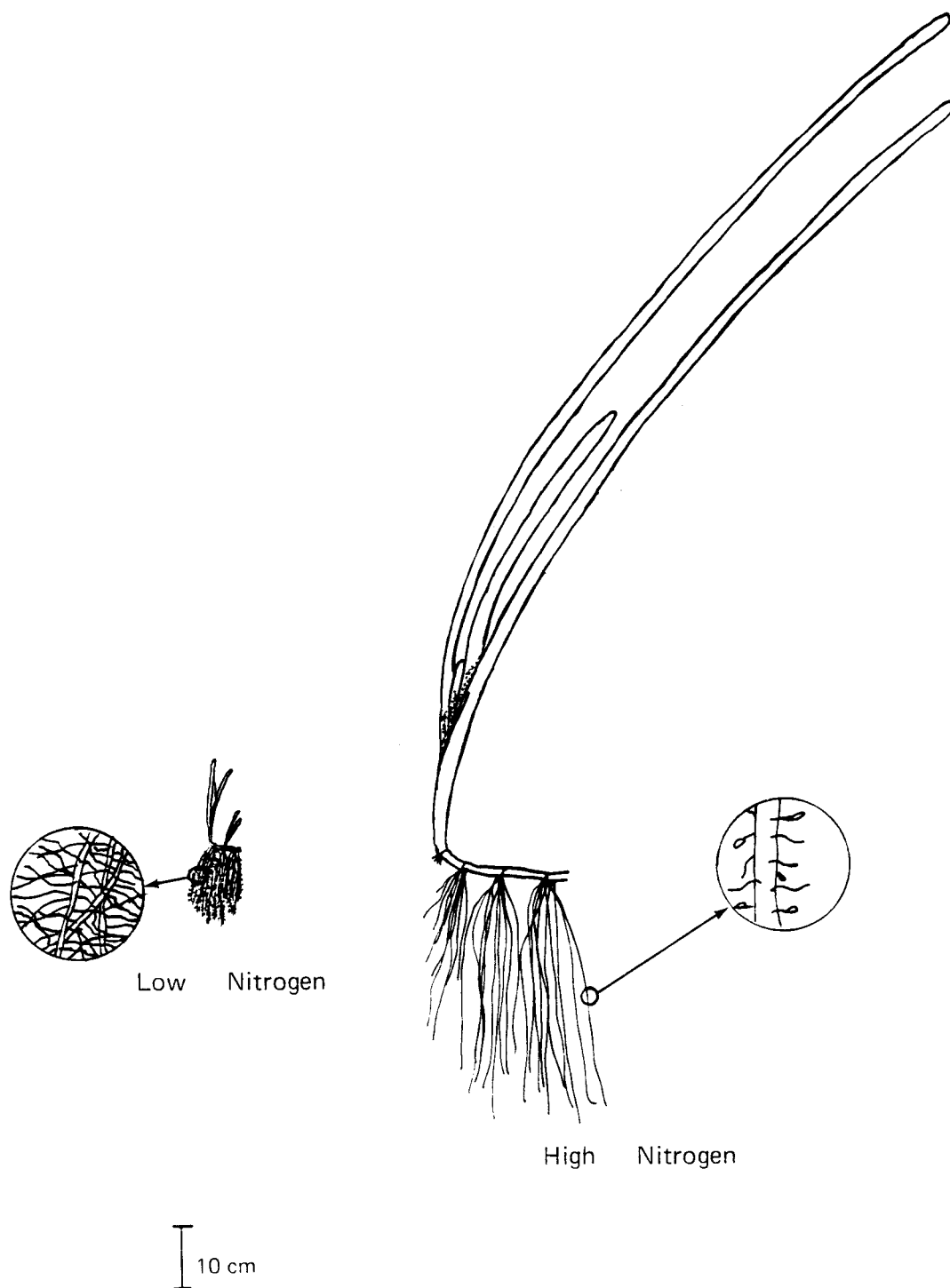


Figure 3.3. Schematic diagram of eelgrass shoots in environments of low and high sediment nitrogen. Leaf, rhizome, and root structure are shown in relative proportion with extensive root hairs on the small branching plants and reduced root hairs on the large plants.

have shown seasonal correlations of eelgrass standing stock to the environmental variables of light and temperature. It was concluded that vegetative growth is primarily controlled by total radiation (Sand-Jenson 1975); that insolation controls shoot density and vegetative reproduction (Jacobs 1979); that temperature and photoperiod strongly influence reproductive growth (Short 1975). In addition, evidence for the environmental control of leaf size and flowering phenology has come from eelgrass transplant experiments (Phillips 1980).

The consideration of only climatic factors as environmental variables is a shortcoming in these attempts to understand the controls on eelgrass standing stock. The importance of nutrient availability (Chapter 2) and nutrient utilization (Chapters 4 and 5) in eelgrass beds shows an additional environmental control on eelgrass growth and biomass. To examine the relation between nitrogen and the form and size of eelgrass beds, various morphological aspects of eelgrass plants are correlated to the size of the sediment interstitial ammonium pool. Similar to other environmental assessments, this analysis suffers from the overlapping influence of many environmental factors. However, in this study the selection of sampling stations within an eelgrass meadow that represent an environmental gradient from nitrogen-poor (low N) to nitrogen-rich (high N) helped to delineate various environmental influences.

#### Shoot Morphology

The size of eelgrass leaves and shoots is controlled by light intensity, temperature, and nutrients as in terrestrial plants, although

submersion in seawater alters the effects of these factors. A useful perspective has developed from extensive studies of agricultural crops: "The potential for development of a leaf is set primarily by irradiance and temperature but its realization depends on nutrient supply" (Milthorpe and Moorby 1974).

The observed difference in leaf size across the tidepool eelgrass meadow correlates with the sediment ammonium pool size and the water depth (Fig. 3.4). The relationship is different in the subtidal eelgrass bed where the smaller change in leaf size may be caused by the difference in available light (Dennison 1979). The differences in the underground plant structure are as striking as the dramatic differences in leaf characteristics (Fig. 3.3). The smaller plants from the nitrogen-poor shallow tidepool have small rhizomes and roots with numerous root hairs, while the larger plants in the deep tidepool and subtidal zone have large rhizomes and coarse roots with no obvious root hairs.

Eelgrass leaf area per shoot in Izembek Lagoon (Dennison 1979) was generally larger in eelgrass beds having more sediment nitrogen (Fig. 3.1a). Similar results have been found in several terrestrial plants, e.g. in sugar beets and potatoes (Watson 1963) and in timothy, cocksfoot, perennial ryegrass, wheat, and several varieties of barley (Langer 1966).

A major structural component determining eelgrass leaf area per shoot is the length of the mature eelgrass leaves. Leaf length data from Izembek Lagoon depict the same relationship to sediment ammonium pool found for leaf area (Fig. 3.1a, b) suggesting an influence of nitrogen on the leaf length in the tidepool eelgrass meadow. These

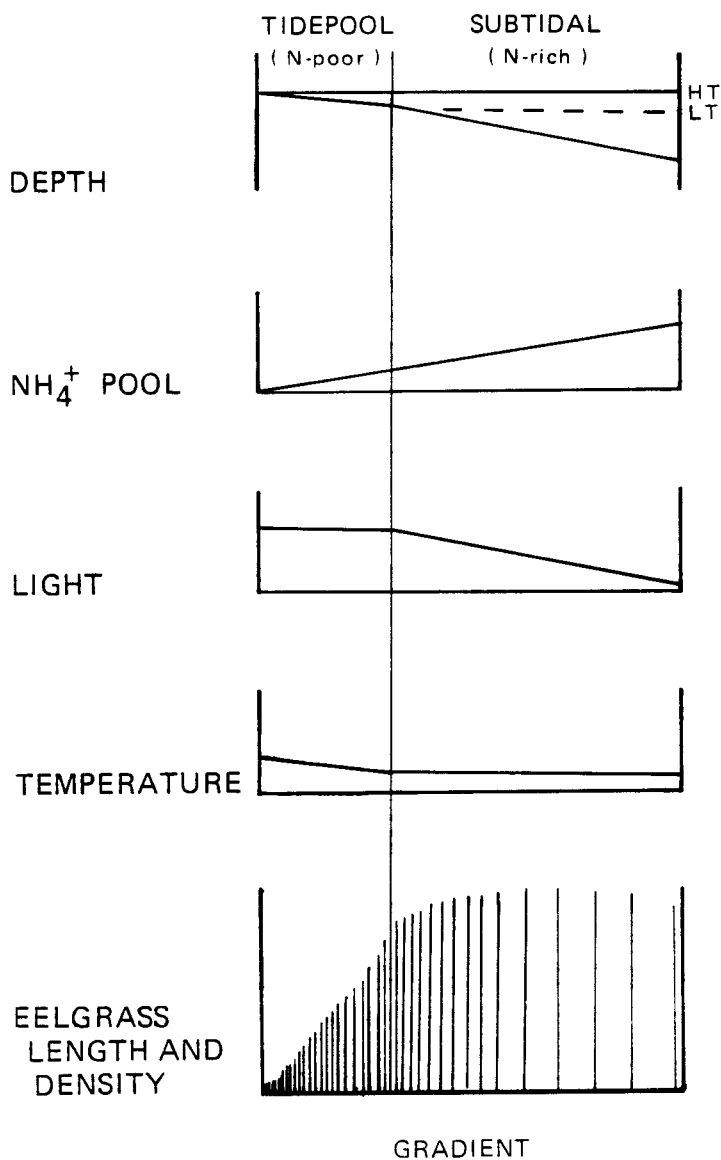


Figure 3.4. A schematic diagram showing the trends in environmental factors across a tidepool eelgrass meadow (nitrogen-poor) and a subtidal meadow (nitrogen-rich). Relative water depth is shown at low tide (LT) and high tide (HT). The increasing sediment interstitial ammonium pool ( $\text{NH}_4^+$  pool) is established with a constant slope. Observed trends in light and temperature (McRoy and Klug unpublished) are set relative to  $\text{NH}_4^+$  pool. Eelgrass leaf length (line height) and shoot density (line closeness) are sketched relative to  $\text{NH}_4^+$  pool.

findings are supported by an enrichment experiment in which the addition of fertilizer containing nitrogen to an eelgrass bed produced a substantial increase in eelgrass leaf length and biomass (Orth 1977). In salt marshes an increase in leaf growth in short *Spartina alterniflora* was observed after the addition of nitrogen fertilizer, but no response was observed in tall *S. alterniflora* (Gallagher 1975).

The schematic diagram showing environmental influences on the tidepool eelgrass meadow indicates that the other major factor likely to affect leaf length is water depth (Fig. 3.4). Eelgrass leaves in the intertidal zone grow longer in areas of greater water depth. The same effect was observed across a shallow eelgrass meadow (depth less than 1 m) in Humbolt Bay, California (Keller and Harris 1966). At Roscoff, France, the effect of water depth on eelgrass length was believed to depend on the duration of water coverage (Jacobs 1979). Whether the relationship between leaf length and water depth is the result of a physical restriction of water level or the effect of tidal exposure is unclear; it appears that tidal exposure could be more important since, with the tidal influences removed, eelgrass leaves in culture experiments can grow longer than the water depth (McMillan 1978).

Eelgrass leaf length in the subtidal (nitrogen-rich) beds indicates a different relationship to sediment ammonium and to water depth than in the tidepool environments (Fig. 3.4). The important environmental factor in subtidal beds, apparently dominating the influences of nitrogen and water depth, is the attenuation of light. Short *et al.*

(1974) experimentally showed the importance of light effects in subtidal eelgrass beds; leaf length was less when light levels were reduced by shading.

The width of eelgrass leaves, another major component of leaf area per shoot, is greater in eelgrass beds having greater sediment ammonium in the nitrogen-poor environment, but in all the nitrogen-rich beds the leaf width appears nearly constant (Fig. 3.1c). Leaf width is a useful index of the sediment nitrogen environment since eelgrass leaves in culture were not affected by temperatures of 10° to 17.5°C, and would not vary extensively during the summer (McMillan 1978). Similar to leaf length, eelgrass leaf width showed an increase with the experimental addition of fertilizer to sediments (Orth 1977).

Thus, the maximum leaf size of an eelgrass shoot in the intertidal zone could be related to either the water depth or the nitrogen supply available in the sediments or both. However, in the subtidal area leaf size appears to be limited by the amount of light reaching the plant.

#### Plant Morphology

Eelgrass vegetative shoot density as a measure of standing stock has been examined in a number of experimental and survey studies. The measurement of shoot density per unit area is an indicator of eelgrass morphology, since the number of shoots in a given area is primarily determined by the extent of lateral branching in the rhizome of the parent plant. Thus new shoot production on existing plants creates a high shoot density and lack of branching creates low shoot density. Density in eelgrass beds can also increase by seed germination; however,

in all the established eelgrass beds examined in Izembek Lagoon seedling counts were a small fraction of shoot density.

The observed shoot density across the tidepool eelgrass meadow in Izembek Lagoon did increase dramatically toward the deep end of the transect, though the light reaching the top of the canopy and the exposure at low tide were approximately the same throughout (Fig. 3.4). Obviously some factor other than light influenced eelgrass density in this tidepool environment. At the reduced light levels in the subtidal eelgrass beds, where nitrogen is abundant, shoot density is probably under light control (Fig. 3.4).

Greatest shoot production was found in association with high light intensity in a number of crop species, and it was also noted that shading only the leaf sheath reduced the formation of new shoots (Evans *et al.* 1964). In eelgrass, shoot density under the relatively uniform light conditions of the tidepool could be influenced by the size of the leaves produced. The larger leaves in a nitrogen-rich eelgrass meadow would shade the leaf sheath which could discourage the plants from producing new shoots. Thus, this biotic feedback could relate shoot density to nitrogen supply by way of leaf size.

The relationship for shoot density and the ammonium pool in natural eelgrass environments demonstrates the influence of availability of nitrogen in the sediments on eelgrass standing stock. However, a problem arises when this significant correlation between shoot density and sediment ammonium is compared to the results of experimental enrichment studies. Two months after the addition of fertilizer to an eelgrass



bed shoot density had increased in comparison to a control plot (Orth 1977). According to the ammonium-density relationship (Fig. 3.2a) shoot density is expected to decrease. This disparity requires further discussion although it is not a new phenomenon in plant studies concerning soil mineral concentrations and the addition of fertilizers (Milthorpe and Moorby 1974). The effect of increasing the nutrient supply on shoot (tiller) density of crop plants was reviewed by Langer (1966), who concluded that shoot density was strongly affected by the level of nutrient supply. These experimental studies, similar to Orth's (1977), added fertilizer to growing plants to increase the nitrogen supply, producing an increase in plant density. Contrary to this, two studies occur in the crop literature in which the nitrogen supply was available to the plant before growth started. In the first study, barley was grown in two lots: one lot received all its nutrients before germination, the other received an equal amount of nutrient divided into weekly doses (Aspinall 1961 in Langer 1966). This experiment showed that plants given weekly enrichments produced six times as many shoots per plant as plants with initially supplied nutrients. The second case involved planting flowers in abandoned fields having a steep fertility gradient (Yoda *et al.* 1963 in White and Harper 1970). The density of plants per square meter showed an inverse logarithmic relationship to fertility; that is, increased density in beds of decreased fertility. Both of these studies disagree with the general observations that nutrient supply increases shoot density and in fact suggest the opposite effect.

The answer to this contradiction of observed shoot density for both eelgrass beds and field crops may lie in the nature of the nitrogen supply and the time scale of response. If the nitrogen supply to the plants is increased by addition of fertilizer, the plants initially respond by producing new shoots. If the nitrogen supply is initially present in the environment, areas of greater nitrogen supply produce fewer shoots than low-nitrogen areas.

In a low-nitrogen environment, production of high shoot density is advantageous to the plant since an increase in density (and subsequently in number of roots) results in an increase in nitrogen absorption from the environment (Watson 1963; Chapin *et al.* 1980). Hence, eelgrass plants can increase nitrogen absorption by increasing lateral branching of the rhizome and thus increasing shoot density. Increased shoot density becomes self defeating when the shoots begin to shade each other and decrease the active leaf area. This situation could occur when the leaf size increases at higher sediment ammonium levels and thus the shoot density decreases. The result of the leaf size and density interaction must then be a trade-off between obtaining the maximum light energy and simultaneously tapping the nitrogen resource in the most advantageous way. This balance between shoot density and leaf size could suffer from the addition of fertilizer, since the plant response of increased size and increased density could lead to overcrowding and degradation of the eelgrass bed.

Eelgrass spadix and flower production are seasonal phenomena believed to be related to seasonal light and temperature cycles (Phillips

1980). Spadix density in Izembek Lagoon during June and July (Fig. 3.2b) reflects the pattern of shoot density (Fig. 3.2a). Little or no flowering of the low-density eelgrass beds was found in the area of high sediment ammonium. Maximum flowering was observed in the nitrogen-poor eelgrass beds having very high shoot density. The amount of flowering in subtidal eelgrass beds could be related to available light, since shading the plants reduced flower production (Backman and Barilotti 1976).

The growth of underground rhizome in eelgrass is directly related to the production of leaf material, since for each leaf that is produced a new section of rhizome is laid down in the sediments. Rhizome growth in terrestrial plants is affected by day length, light intensity, and temperature (Evans *et al.* 1964). As with leaf production, these climatic conditions account for much of the seasonal change observed in rhizome length (Short 1975; Jacobs 1979). Light is the only one of these factors that would contribute to the spatial differences observed in Izembek Lagoon, since photoperiod and temperature are relatively constant. But light does not appear to be a spatial control since rhizome length is smallest in the tidepool having high light intensity.

The environmental nitrogen supply correlates with rhizome length for both the tidepool and subtidal eelgrass beds. The similar graphs for leaf width (Fig. 3.1c) and rhizome length (Fig. 3.2c) demonstrate a close relationship between the leaf size and the size of the rhizome produced.

Root structure has been studied only briefly in eelgrass beds (Conover and Gough 1966; Smith *et al.* 1979); however, there is an extensive literature on terrestrial plant root systems (Clarkson 1974; Nye and Tinker 1977).

The functional importance of root structure in eelgrass beds appears related to the sediment environment and, most importantly, to the nitrogen supply. Acquisition of nitrogen from the sediment interstitial water is dependent on two major factors: (1) the concentration of nitrogen in the interstitial water (Chapter 2), and (2) the size of the rhizosphere (i.e. the volume of sediment that is directly accessible to the root and root hairs; Clarkson 1974). The root system in the low-nitrogen environment having a large rhizosphere volume extends throughout the sediment where mineralization occurs. Less root hair development in high-ammonium conditions could partly result from toxic effects on plant tissue (Haynes and Goh 1978) and from the plants' having higher concentrations of nitrogen more readily available. The size of the root system is larger in high-nitrogen areas than in the low-nitrogen environments, as is the entire plant, but its structure is simpler.

#### SUMMARY

Sediment nitrogen was correlated with the morphology of eelgrass leaves and roots. Generally, the interaction appears similar to the situation in terrestrial plants: higher nitrogen results in larger plants. However, in eelgrass environments a distinction can be made

between eelgrass beds in shallow water and deep water beds which are restricted by light.

A gradient of environmental conditions was defined by the pool of interstitial ammonium in the sediment, encompassing eelgrass beds across a shallow tidepool within the intertidal zone and into deepening subtidal areas. These environments represent areas in which sediment nitrogen and other chemical compounds vary and light is constant (tidepool) and areas where the sediment chemistry and light are both variable (subtidal). The two extremes include eelgrass plants of different morphological structure (Fig. 3.3).

High shoot density and plants with short, narrow leaves and fine roots having extensive root hairs were found in the shallow nitrogen-poor eelgrass beds, whereas at the deepest end of the tidepool large wide-leaved plants were observed. Light variations were minimal in the tidepool environment; however, leaf size was greater in tidepool beds of higher sediment nitrogen and greater water depth. The root and rhizome system was small but well developed in the nitrogen-poor sediments and showed less structure but larger size in the nitrogen-rich environment.

The environmental characteristics of the subtidal eelgrass bed differ greatly from those of the tidepool as a result of the attenuation of light with increasing depth. Within this subtidal environment plant morphology was not strongly correlated with sediment nitrogen. Leaf size and shoot density appear to be controlled by the limited light supply.

Enrichment of eelgrass beds with fertilizer causes an increase in leaf size similar to agricultural crops, which supports the hypothesis that nitrogen availability affects morphology. The response of eelgrass shoot density to fertilizer addition was contrary to the significant relationship between density and nitrogen. Application of fertilizer to crop plants and eelgrass shows an immediate response of new shoot production, but this is not the equilibrium response of plants growing in already nitrogen-rich environments, illustrating the importance of the nature of the nitrogen supply to the plants and the time scale of the response.

## CHAPTER 4: NITROGEN UPTAKE BY LEAVES AND ROOTS OF EELGRASS, *ZOSTERA MARINA* L.

### INTRODUCTION

Nutrient uptake by the seagrass, *Zostera marina* L. (eelgrass), occurs at the surface of leaves and roots; the nutrients are then translocated throughout the plant (McRoy and Barsdate 1970; McRoy and Goering 1974; Iizumi 1979). Considerable nitrogen uptake by leaves and roots of eelgrass is required to maintain plant growth at the high primary production rates observed in eelgrass beds (McRoy and McMillan 1977). Examination of the relationship between uptake in the leaf and root zones and the availability of nitrogen resources enables an evaluation of the influence of nitrogen on eelgrass growth.

Water column nitrogen is supplied to the plants by tidal exchange in relatively uniform concentrations across an eelgrass meadow (Chapter 2). However, the spatial distribution of eelgrass is variable within eelgrass meadows and appears related to the nitrogen pool size in the sediments (Chapters 2 and 3). The dominant form of nitrogen in anoxic eelgrass sediments is ammonium; nitrate and nitrite can occur at low concentrations in a thin oxidized layer around the roots (Iizumi *et al.* 1980). Enrichment of nutrients in the water column (Raymont 1947) and in the upper layer of sediments (Orth 1977) of eelgrass beds stimulated plant growth. These experiments, together with manipulation studies of the plant-ammonium pool interaction (Chapter 5), demonstrate the possibility of nitrogen limitation in eelgrass beds.

An analysis of the nitrogen available to the plants (Chapter 2) and the kinetics of nitrogen uptake is fundamental to the consideration of nitrogen limited growth. Three aspects of nitrogen kinetics in eelgrass leaves are proposed to illustrate different processes in nitrogen uptake (Fig. 4.1). The rate of movement of nitrogen from the water into eelgrass leaves over a short time period is defined as "1 hr uptake". This uptake includes the initial adsorption of nitrogen onto the porous cuticle of the leaf surface occurring within the first few minutes of an experiment and the absorption of nitrogen into the leaf.

Eelgrass is assumed to be similar to most higher plants in which cell walls have a high ion exchange capacity, and labelled ions exchange quickly with the unlabelled ones already on the cell wall (Clarkson 1974). Further, the quantity of material adsorbed onto the cell surface in this manner can be determined from a plot of accumulation vs. time. An alternative hypothesis is that these "adsorbed ions" move into an internal cell pool rather than remaining at the cell surface. Similar to the cell surface hypothesis, such an internal pool could exchange with the external ion concentration while providing an ion solution available to the plants. The initial uptake through "adsorption" occurs in the accumulation experiments during the first 10 to 15 min after addition of the labelled nitrogen (Fig. 4.1). Adsorption at the beginning of an uptake experiment was observed in rice roots for both ammonium and nitrate uptake (Fried *et al.* 1965). The actual rate of nitrogen uptake into the leaves is expressed by the slope of the line representing accumulation by absorption vs. time (Fig. 4.1). I examined the



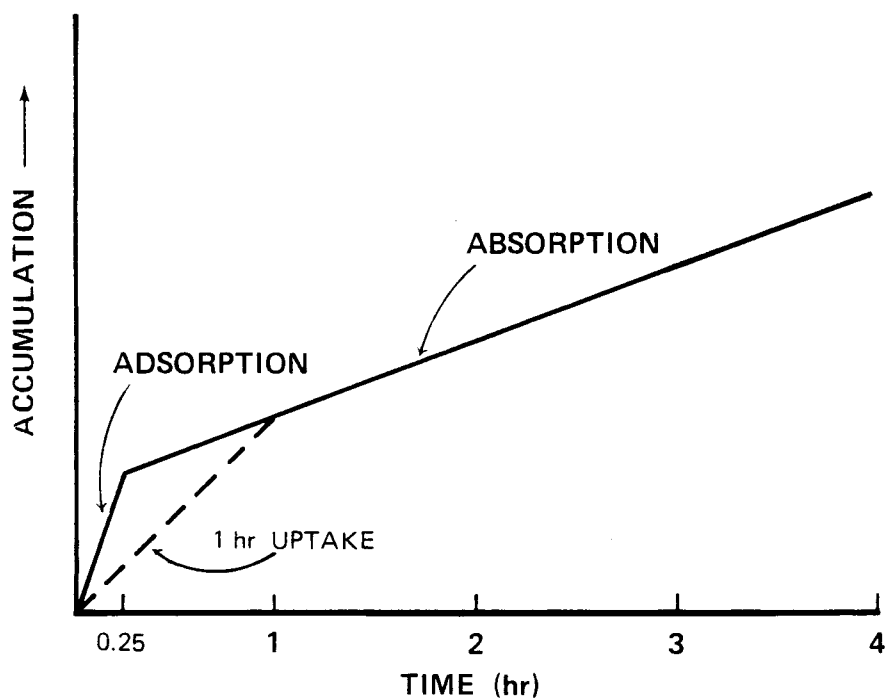


Figure 4.1. Schematic presentation of accumulation vs. time showing the adsorption phase and absorption phase of accumulation. The "1 hr uptake" rate is the slope of the accumulation curve after one hour.

kinetics of ammonium and nitrate uptake from the water column by eelgrass leaves and the uptake of ammonium by roots from the sediments.

## METHODS

### Study Area

The eelgrass meadows at Izembek Lagoon on the north side of the Alaska Peninsula were the site for this investigation. The extensive stands of eelgrass that dominate the lagoon offered a wide range of plant and environmental characteristics for study. The collection and experimental areas were located in the vicinity of Grant Point, Izembek Lagoon (Fig. 2.1).

### Experimental Methods

An experimental technique was designed to measure the *in situ* nitrogen uptake by the leaves during 1 hr incubations while the roots remained undisturbed in the sediments (ampule experiments). The leaves of one shoot were encapsulated in a water-filled glass ampule (1 or 0.25 liters) and sealed with a rubber stopper and silicon grease. Time series experiments to measure ammonium accumulation consisted of leaves incubated in ampules *in situ* from 15 min to 2 hr at low tide while remaining attached to the undisturbed rhizome. Nitrogen,  $^{15}\text{N-NH}_4^+$  or  $^{15}\text{N-NO}_3^-$ , was added to the ampule with a syringe and mixed throughout for each experimental treatment (Table 4.1). The ampule experiments were terminated by digging up the attached rhizome and roots, draining the  $^{15}\text{N}$  labelled water from the ampule, and transporting the plants in the ampule back to the laboratory at Grant Point for processing as described below.

Table 4.1. List of  $^{15}\text{N}$  uptake experiments and environmental conditions at Izembek Lagoon, Alaska.

Date	Station	Nutrient Added	Added Concentration (μM)		Temp °C	Light* ly/hr	Type of Uptake Experiment
Chamber Experiments							
12 June 76	G	NH <sub>4</sub> <sup>+</sup>	0.7	8	12.5	88.9	Time Series, Leaf
15 June 76	G	NH <sub>4</sub> <sup>+</sup>	0.0	8, 40, 60, 160	13.0	66.3	Root
16 June 76	G	NH <sub>4</sub> <sup>+</sup>	1.3	8, 160, 240	14.0	25.5	Leaf & Root
17 June 76	G	NH <sub>4</sub> <sup>+</sup>	4.0	8, 60, 160, 240	9.2	65.3	Leaf & Root
18 June 76	G	NH <sub>4</sub> <sup>+</sup>	10.0	8, 60, 160, 240	8.6	45.0	Leaf & Root
Ampule Experiments							
18 July 77	7	NH <sub>4</sub> <sup>+</sup>	9.0	0	21.0	21.9	Time Series, Leaf
25 July 77	4	NH <sub>4</sub> <sup>+</sup>	1.0 - 5.0	0	16.0	13.5	Leaf
27 July 77	7	NH <sub>4</sub> <sup>+</sup>	1.0 - 7.0	0	17.5	-	Leaf
27 July 77	7	NO <sub>3</sub> <sup>-</sup>	1.0 - 19.0	0	17.5	-	Leaf
30 July 77	15	NH <sub>4</sub> <sup>+</sup>	1.0 - 4.0	0	15.0	-	Leaf
30 July 77	15	NO <sub>3</sub> <sup>-</sup>	1.0 - 8.0	0	15.0	-	Leaf
4 Aug 77	3	NH <sub>4</sub> <sup>+</sup>	3.5	0	14.5	-	Time Series, Leaf
4 Aug 77	3	NO <sub>3</sub> <sup>-</sup>	1.0 - 7.0	0	14.5	-	Leaf

\* Irradiance received during incubation

Nitrogen uptake was also measured in partitioned chambers (after McRoy and Goering 1974) with leaves under natural light conditions at the Grant Point laboratory. The plants were removed from the substrate at Station G, a subtidal eelgrass bed; the intact roots and rhizomes were cleaned of sediments and the leaves were wiped free of epiphytes; the plants were placed in partitioned seawater-filled chambers with the rhizomes and roots suspended in the darkened lower section in oxygen-free water. Ammonium labelled with  $^{15}\text{N}$  was added in a variety of treatments to the leaf and/or the root zone (Table 4.1).

The eelgrass leaves and roots from both types of  $^{15}\text{N}$  experiment were removed from the containers, separated, rinsed in fresh water and dried at  $90^{\circ}\text{C}$  for 24 hr. Plant samples were then weighed, ground into a powder, and stored in a desiccator for future  $^{15}\text{N}$  and total nitrogen content analyses.

Environmental conditions were monitored during individual uptake experiments. Ammonium concentrations in the water column were determined colorimetrically (Koroleff 1976) for the filtered seawater used in each uptake experiment. Solar radiation for the duration of the plant incubation was measured with a continuous recording radiometer (Kahl Scientific Inst. Corp., California). Temperature in the chamber was measured at the beginning of each incubation; temperature in the ampule experiment incubated *in situ* was measured in the water column at the start of the experiments.

## Analytical Methods

Nitrogen content of the plants was determined by Dumas combustion using a Coleman Nitrogen Analyzer. The automated Dumas method was used to convert the  $^{15}\text{N}$  labelled plant samples into  $\text{N}_2$  gas for  $^{15}\text{N}$  analysis (after Barsdate and Dugdale 1965). The  $\text{N}_2$  gas was pumped directly into a Jasco N-15 Analyzer through a glass inlet system (similar to Wada *et al.* 1977; Appendix A). Atom percent  $^{15}\text{N}$  was calculated directly from multiple emission scans of the N28, N29, and N30 wave lengths (Lloyd-Jones *et al.* 1974). The nitrogen uptake rate was then calculated from the atom percent  $^{15}\text{N}$ , the nitrogen content of the sample, and the duration of the experiment (Dugdale and Goering 1967).

## RESULTS

### Ampule Experiments

The leaves of eelgrass took up both ammonium and nitrate from the water column (Fig. 4.2). The rate of leaf uptake of these ions during one hour *in situ* incubations was directly related to the nitrogen concentration in the ampule. The water temperature (Table 4.1) had a variable influence on uptake, although a trend of increased uptake with increasing temperature was indicated. The relationship between uptake and concentration is linear over a range of water column concentrations ( $\text{NH}_4^+-\text{N} \approx 1.0$  to  $12.0 \mu\text{M}$  and  $\text{NO}_3^--\text{N} \approx 0.8$  to  $19.0 \mu\text{M}$ ). Linear regression of these data shows that the slope for ammonium ( $a = 0.80 \text{ } \mu\text{g}^{-1} \text{ hr}^{-1}$ ) is greater than that for nitrate ( $a = 0.47 \text{ } \mu\text{g}^{-1} \text{ hr}^{-1}$ ). The graphs of both the ammonium and nitrate uptake rates vs. concentration have a positive intercept.

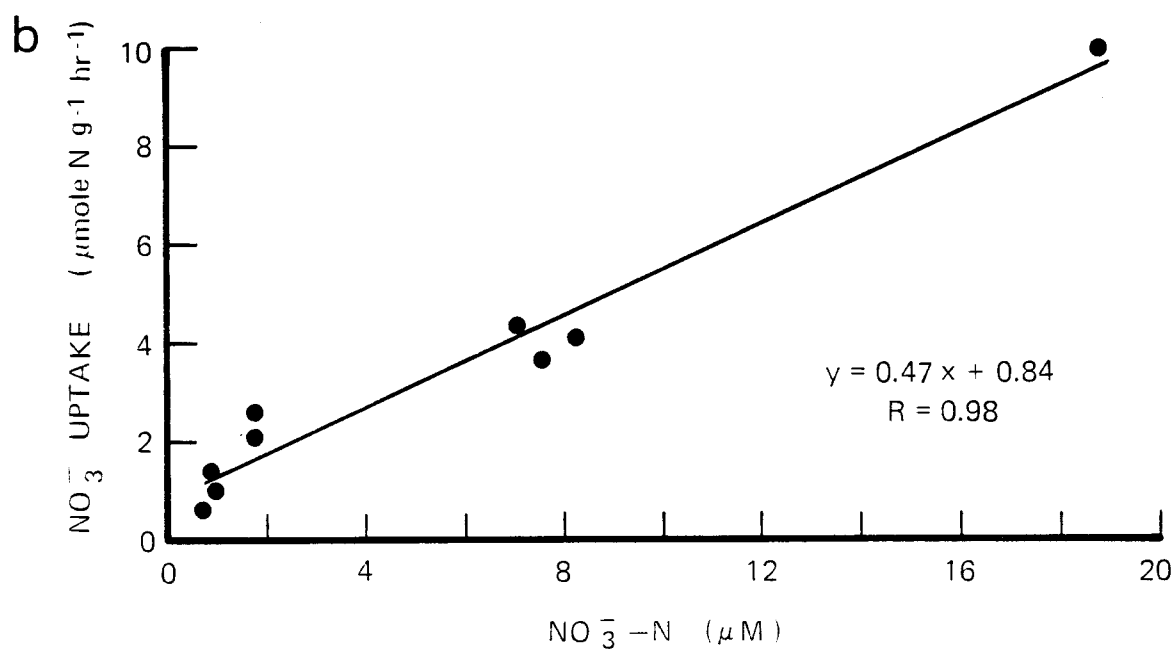
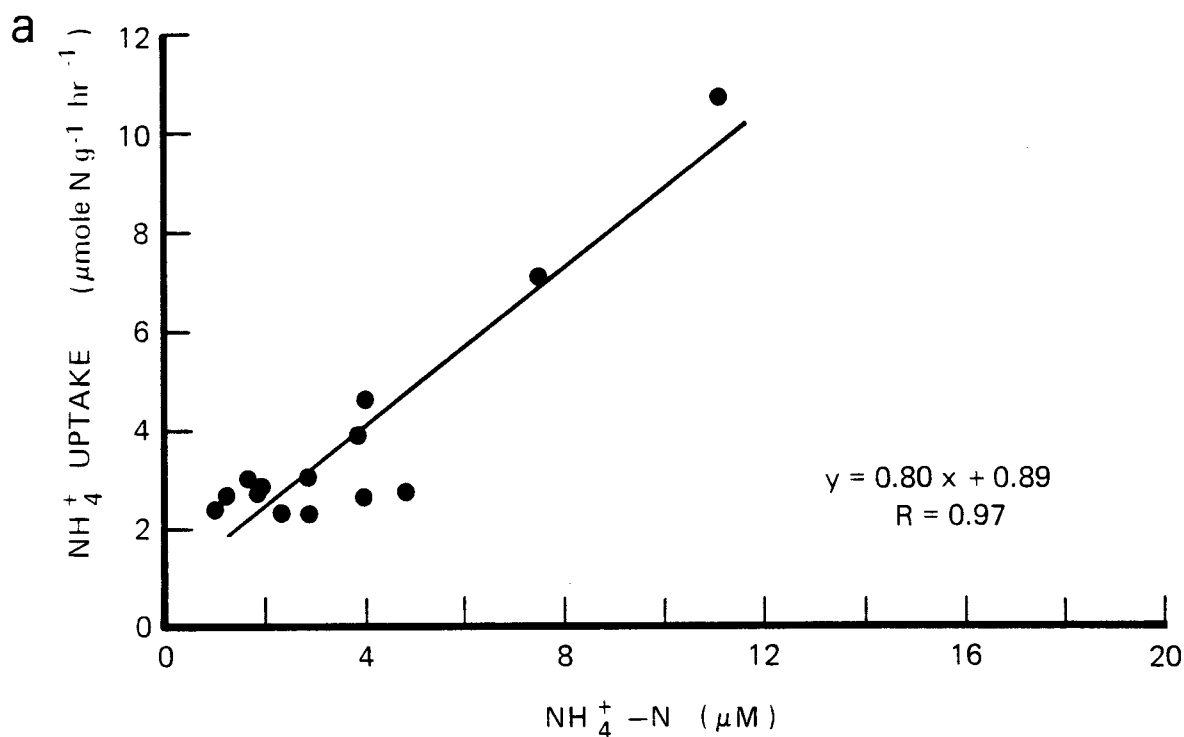


Figure 4.2. Uptake rate of nitrogen per gram dry weight from the water column by eelgrass leaves as a function of concentration for 1 hr incubations on individual leaves in the ampule experiments: (a) Ammonium uptake vs. ammonium concentration; (b) Nitrate uptake vs. nitrate concentration.

Time series incubations performed on *in situ* plants illustrated the accumulation of ammonium in eelgrass leaves for different time periods and at different concentrations. The leaves rapidly accumulated ammonium by adsorption in the first 15 min of an experiment, and accumulated at a slower constant rate by absorption for the next 2 hr (Fig. 4.3a). The slope of the absorption part of the curve is greater at higher ammonium concentrations.

#### Chamber Experiments

Ammonium accumulation by the leaves was also measured in the partitioned chambers for a time series (up to 25 hr) at low ammonium concentrations (Fig. 4.3b). The first leaf sample in this series showed substantial adsorption in the initial 12 min of incubation. This rapid adsorption was followed by constant slower absorption for 14 hr, after which no further accumulation occurred. This accumulation pattern, similar to that for the *in situ* ampule experiments, showed a lower absorption rate (Fig. 4.3b) after the initial rapid adsorption. The combination of the results from the three accumulation experiments, each enriched to different concentrations, shows that absorption rates (Fig. 4.3a, b) are directly related to ammonium concentration. This relationship between absorption and concentration has a significant linear correlation, with a regression coefficient of 0.45 and a near-zero intercept (Fig. 4.4).

The simultaneous uptake of ammonium into leaf and root tissue was determined by 4 hr incubation under controlled conditions by adding labelled nitrogen to both upper and lower chambers (Table 4.1). The

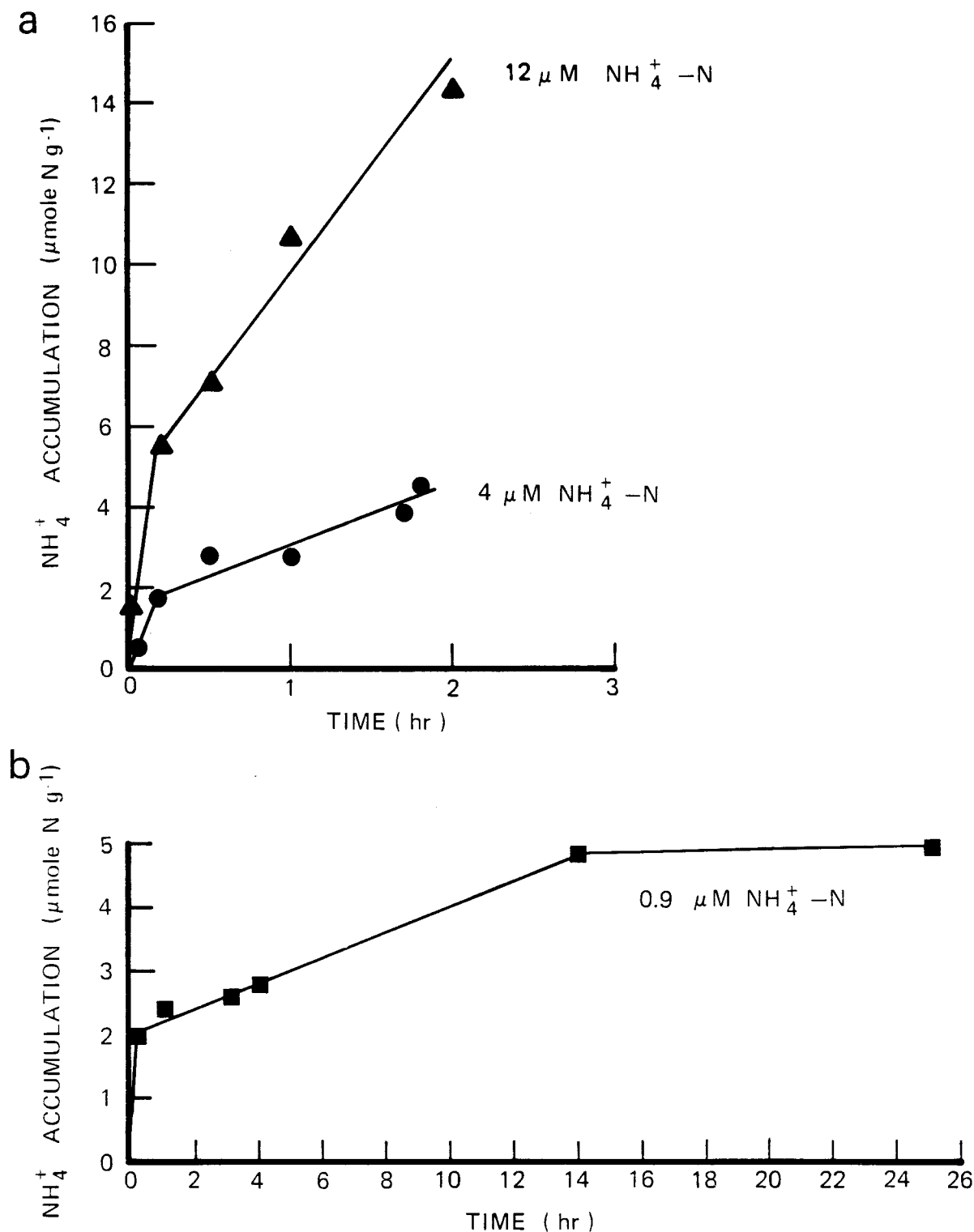


Figure 4.3. Accumulation of ammonium per gram dry weight from the water column by eelgrass leaves as a function of time (individual leaves). Initial rapid accumulation for the first 15 min followed by slower absorption into the leaf: (a) 2 hr incubations at ammonium concentrations of 4 and  $12 \mu\text{M}$ ; (b) 24 hr incubation at ammonium concentrations of  $0.9 \mu\text{M}$ , with reduced accumulation after 14 hr.



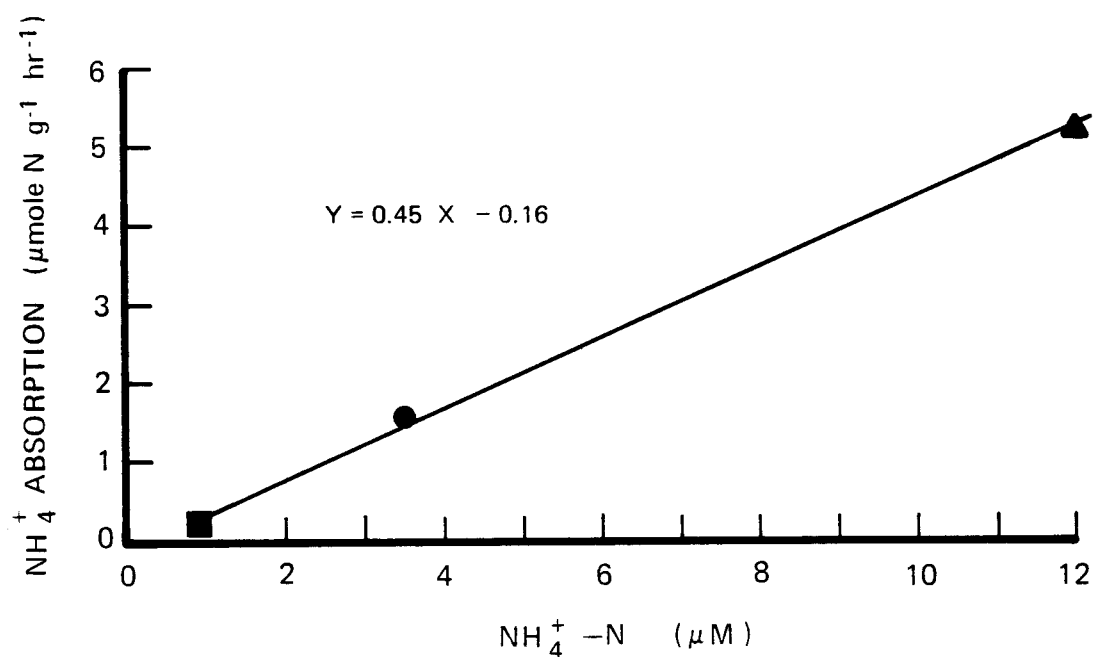


Figure 4.4. Absorption rate of ammonium per gram dry weight from the water column by eelgrass leaves is calculated from the slope of the plots in Fig. 4.3. The slope of absorption is  $0.45 \text{ g g}^{-1} \text{ hr}^{-1}$  and the intercept is near zero.

rates of uptake by leaves increased with increased ammonium concentration at all but the highest level (Table 4.2), but there was no statistically significant difference in leaf uptake at any of the root enrichment experiments (two way analysis of variance with blocking, see Table A.3 in Appendix A). Increased temperature and light (Table 4.1) appeared to promote root uptake but the effect was not significant.

The contribution of leaves and roots to ammonium uptake by the whole plant was analyzed by adding the uptake rates for the leaf and root part of each experimental condition (Table 4.2). Ammonium uptake by the whole plant ( $\text{g N} \cdot \text{g plant N}^{-1} \cdot \text{hr}^{-1}$ ) was greater when plants were exposed to higher leaf zone and higher root zone ammonium concentrations (Fig. 4.5). The slopes of the regression lines for the high and low leaf zone concentrations were not significantly different ( $P = 0.25$ ), but the intercepts were significantly different at  $P = 0.005$  (Snedecor and Cochran 1973). The similar slopes indicate that ammonium uptake by roots is independent of leaf zone concentrations; the distinct intercepts demonstrate that higher water column ammonium concentrations increase the rate of uptake by the plants.

#### DISCUSSION

The nitrogen necessary to satisfy the metabolic requirements of eelgrass growth can be obtained by adsorption of ammonium and nitrate ions to leaf or root surfaces and subsequent absorption into the plant tissue. The rate at which nitrogen ions contact the plant surface is determined by water column nitrogen concentration and by the rate of molecular diffusion to the plant surface. Presumably the rate of

Table 4.2. Ammonium concentrations and uptake rates for combined leaf and root experiments from the chamber experiments, June 15-18, 1976.

	n	$\text{NH}_4^+-\text{N}$ ( $\mu\text{M}$ )	Uptake Rate ( $\mu\text{mole g}^{-1} \text{ hr}^{-1}$ )	(95% CI)
Leaves	12	0.8	0.52*	(0.10)
	9	1.8	1.05	(0.12)
	8	4.4	3.14	(0.28)
	8	10.6	3.18	(0.41)
Roots	10	8.6	0.88	(0.13)
	3	40.8	1.41	(0.52)
	7	60.6	1.46	(0.33)
	10	160.6	2.22	(0.45)
	6	240.5	2.93	(0.85)

\* Nitrogen translocated from roots since no  $^{15}\text{N}$  was added to the leaf zone in this experiment.

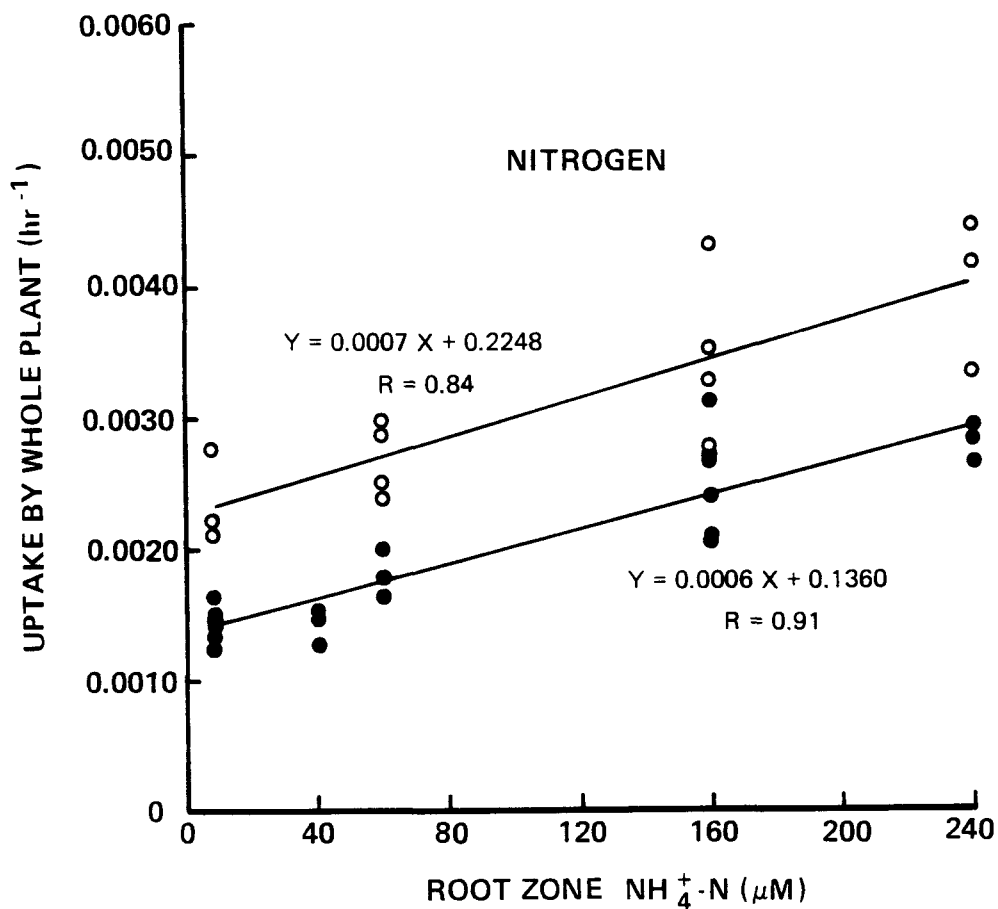


Figure 4.5. Whole plant nitrogen uptake as a function of ammonium concentration in the root zone for individual experiments. Regression lines indicate statistically significant uptake rates for low leaf zone ammonium concentrations of 0 and 1.3  $\mu\text{M}$  (●) and high leaf zone ammonium concentration of 4.0 and 10.0  $\mu\text{M}$  (○).

nitrogen ion movement into the internal cell pool is determined by the number and activity of sites available for ion transfer, the ion concentration at these sites, and the degree of saturation in the cells. If the absorption into the internal cell pool limits the uptake of nitrogen in eelgrass, then the relationship between uptake rate and concentration is hyperbolic (Michaelis-Menten). If the ion absorption is controlled by external concentration and the diffusion process, this relationship is linear.

#### Nitrogen Uptake by Leaves

The uptake of nitrogen by eelgrass leaves is dependent on the water column nitrogen concentration. However, the ability of the plant to obtain nitrogen from the water is a function of leaf morphology, physiology, and to a small extent environmental temperature. The leaf structure in these submerged aquatic plants (Doohan and Newcomb 1976; Kuo 1980) appears to be adapted for rapid uptake of both ammonium and nitrate into water-filled spaces on the cell wall and eventually into the plant tissue. The relationship between uptake for nitrate and ammonium uptake and ambient nitrogen concentration during short-term ( $\sim 1$  hr) exposure was linear and showed no evidence of saturation (Fig. 4.2). Thus, nitrogen ion uptake (adsorption of ions onto the cell surface plus absorption of ions into the internal cell pools) by these leaves could allow rapid nitrogen uptake when water with high nitrogen concentration moves across an eelgrass bed.

The ammonium uptake was greater than that for nitrate, indicating a preference for reduced nitrogen. The importance of ammonium as the

major water column nitrogen resource is also indicated by the slope of the 1 hr uptake vs. concentration relationship (Fig. 4.2). A significant ammonium resource for eelgrass is suggested by ammonium generation in the water column creating higher ammonium concentrations compared to nitrate concentrations in Izembek Lagoon during the summer (Fig. 2.3). Although these concentrations are low ( $\text{NH}_4^+-\text{N} \approx 1 \text{ to } 3 \mu\text{M}$ ), the plants could obtain substantial nitrogen from prolonged exposure.

Ammonium uptake in terrestrial plants occurs initially as a result of ion adsorption onto the porous cuticle of the plant surface during the first few minutes of exposure to a nitrogen enrichment (Clarkson 1974). The initial adsorption of labelled nitrogen to the leaf does not appear to be an active process since it is independent of metabolic activity (Epstein 1972), and the ions can be released by exposing the plants to unlabelled solution (Clarkson 1974). The adsorptive process could be an important mechanism for rapidly bringing ammonium ions in contact with the cell membrane where they are available for absorption.

The absorption rate of ammonium by eelgrass leaves was greater for plants incubated with increased concentrations (Fig. 4.3), and the slope of absorption vs. concentration indicated an affinity (Button 1978) for absorption of ammonium ( $a = 0.45$ , Fig. 4.4, where  $a = \mu\text{mole N} \cdot \text{g}^{-1} \text{ hr}^{-1} \div \mu\text{mole N} \cdot \ell^{-1}$ ). This ratio is similar to values for daily ammonium uptake by eelgrass,  $a = 0.3$  (Iizumi 1979) and by another aquatic plant, *Ceratophyllum*,  $a = 0.12 \text{ to } 0.30$  (Toetz 1973).

A concentration-dependent uptake mechanism and a large leaf surface area (Dennison 1979) enable eelgrass to take full advantage of transient water masses containing high nutrient concentration. The

advantage of a water column ammonium supply is decreased at times during the year when epiphyte growth covers the older eelgrass leaves. The reduction in water column ammonium concentration in beds having few epiphytes was frequently evident in Izembek Lagoon when, for example, before slack low tide the  $\text{NH}_4^+\text{-N} = 3.7 \mu\text{M}$ , while an hour later at low tide it was  $1.0 \mu\text{M}$ . These observations suggest that eelgrass leaves and epiphytes, growing under ambient nitrogen concentrations, can effectively utilize water column nitrogen resources. For example, using the relationship for ammonium absorption (Fig. 4.4): (1) If the water column ammonium concentration  $3.7 \mu\text{M}$  was maintained by water flow through the eelgrass bed, one third of the eelgrass nitrogen requirement would be obtained from the water column (based on an average production rate of  $0.003 \text{ g} \cdot \text{g}^{-1} \text{ hr}^{-1}$  and nitrogen content of 2% dry wt, from McRoy and McMillan 1977). (2) If the water column ammonium concentration was  $2.0 \mu\text{M}$  and the production rate was low ( $0.0005 \text{ g} \cdot \text{g}^{-1} \text{ hr}^{-1}$ ), the water column would supply 1.3 times the eelgrass nitrogen requirement. Increased accumulation at high ammonium concentrations (Fig. 4.2a) and continuous accumulation at low levels (Fig. 4.3b) indicate eelgrass functions as an "ammonium sponge" in the water column.

The possible influence of epiphytes on ammonium concentrations in the water column suggests that at times during the year epiphytic algae utilize this nitrogen resource, and that epiphytic animals regenerate ammonium at the leaf surface. An estimate of the epiphytic algal effect was calculated, using observed epiphytic biomass and production rates. Assuming an epiphyte biomass of 24% of the eelgrass standing stock (this is high for Izembek Lagoon) and an observed epiphyte production rate of

0.88 mg C g<sup>-1</sup> hr<sup>-1</sup> (Penhale 1977), the effect of epiphytic utilization of the water column ammonium concentration described above would only account for 28% of the depletion. This does not include ammonium regeneration by epiphytic animals which would decrease this percentage. Although epiphytes could be important at times in Izembek Lagoon, they do not appear to be a major factor in ammonium utilization from the water column.

Measurements of ammonium uptake over 24 hr were in the range of the plants' daily growth requirement (Iizumi 1979). These daily rates are lower than the hourly uptake rates and suggest two conclusions: (1) The concentration-dependent uptake of ammonium could exceed the plant requirement when external concentrations are high. (2) The capacity for rapid uptake is such that eelgrass plants can obtain the required nitrogen in a short-term exposure to high ammonium concentrations. Thus, on a daily basis when production is low, these plants could obtain enough nitrogen through uptake by leaves to meet growth requirements if high nitrogen concentrations occur in the water column during tidal exchange.

#### Ammonium Uptake by Roots

Eelgrass, like most other vascular plants, takes up nitrate and ammonium through its roots and translocates them to the stem and leaves for metabolism (McRoy and Goering 1974). However, in most eelgrass sediments nitrate concentrations are low relative to ammonium concentrations (Iizumi *et al.* 1980) and the uptake of ammonium dominates. In addition, Iizumi (1979) found that nitrate uptake in eelgrass was inhibited by high concentrations of ammonium in the root zone.



The ammonium uptake rate by roots of many terrestrial plants appears to depend on the age of the plant (Joseph *et al.* 1975). Uptake rates for eelgrass roots are similar to those of older citrus roots but less than those for young citrus roots and other young plant roots (Table 4.3). The uptake rates for eelgrass suggest that mature plants are similar to other higher plants in their ability to take up ammonium through the roots.

The suggestion has been made that eelgrass obtains its nitrogen through the roots (McRoy and Goering 1974) but in light of the effective uptake system in the leaves, the possibility of simultaneous ammonium uptake by leaves and roots was examined. The combined results from four root and leaf zone enrichments on four consecutive days show that ammonium concentration in the roots did not significantly affect the uptake rate by the leaves (Table A.3). The uptake rates from the chamber experiments were similar to the *in situ* absorption rates for leaves incubated in different eelgrass beds (Fig. 4.4). Uptake rates for eelgrass roots, on the other hand, were in the same range as other measurements of uptake by roots (McRoy and Goering 1974; Iizumi 1979). The influence of temperature and light on ammonium uptake was less than that of concentration, however these effects may account for much of the variation observed in leaf and root uptake (Table 4.2).

The uptake of ammonium by either the roots or leaves of eelgrass is apparently independent of the rate of uptake by the opposing attached plant part (leaf or root). These results agree with the proposed uptake mechanism, in which the leaves function as a sponge for ammonium, and indicate that uptake by roots is concentration dependent over the lower

Table 4.3. Comparison of average ammonium uptake by roots of higher plants at about 100  $\mu\text{M}$  ammonium concentration.

Plant	Age	$\text{NH}_4^+-\text{N}$ ( $\mu\text{M}$ )	Uptake Rate ( $\mu\text{mole g}^{-1} \text{ hr}^{-1}$ )	Reference
Rice roots*	14 days	100	12.5	Fried <i>et al.</i> 1965
Soybean roots	80 days	120	11.0	Joseph <i>et al.</i> 1975
Citrus roots	60 days	100	11.3	Hassan and Hai 1976
Citrus roots	180 days	100	2.3	"
Eelgrass roots	mature**	160	2.2	This study

\* Excised roots

\*\* Mature plants are older than 1 yr.

range of interstitial concentrations. Experiments at high ammonium concentrations indicate saturation of uptake rate vs. concentration (Iizumi 1979), suggesting that Michaelian kinetics may be appropriate for eelgrass root uptake. The rates of ammonium uptake by roots and leaves imply that eelgrass can monopolize a sporadic water column supply of nitrogen while maintaining a continuous removal of sediment ammonium.

#### Uptake by Whole Plants

The combined leaf and root ammonium uptake rates (rate =  $\text{g N} \cdot \text{g N}^{-1} \cdot \text{hr}^{-1}$ ) are compared to the eelgrass nitrogen requirement. As an example of the importance of nitrogen uptake to eelgrass productivity, the nitrogen requirement was calculated from carbon production rates and an average carbon-to-nitrogen ratio. Productivity rates for eelgrass have been reported from 0.15 to 2.2  $\text{mg C (g dry)}^{-1} \text{ hr}^{-1}$  (McRoy and McMillan 1977). An average plant composition for carbon of 38% dry wt, and for nitrogen of 2% dry wt (McRoy and McMillan 1977) gives an eelgrass carbon or nitrogen uptake rate ( $\text{g C} \cdot \text{g C}^{-1} \cdot \text{hr}^{-1}$  or  $\text{g N} \cdot \text{g N}^{-1} \cdot \text{hr}^{-1}$ ) of 0.0004 to 0.0058  $\text{hr}^{-1}$ . The range of nitrogen required to match these productivity rates exceeds the range of available nitrogen from ammonium uptake (Fig. 4.5). This implies that the high production rates are limited to beds of high interstitial ammonium concentrations, or that nitrate uptake or nitrogen fixation supply some of the nitrogen requirements. Plants growing at low production rates ( $< ca\ 0.001\ \text{hr}^{-1}$ ) have ample nitrogen available from the root zone with ammonium concentrations of 8-240  $\mu\text{M}$  and little nitrogen in the water column. At maximum production rates ( $> 0.005\ \text{hr}^{-1}$ ) insufficient nitrogen is available in these

experimental conditions from either the leaf ( $\text{NH}_4^+\text{-N}$  of 0-10  $\mu\text{M}$ ) or from the root zone ( $\text{NH}_4^+\text{-N}$  of 8-240  $\mu\text{M}$ ) to meet the projected nitrogen requirement, suggesting that uptake by roots at higher concentrations is important.

The middle range of production rates (*ca* 0.003  $\text{hr}^{-1}$ ) match the average experimental conditions at Izembek Lagoon. Extrapolating these uptake rates to the natural environment suggests that plants in nitrogen-poor environments must grow at low production rates because of low nitrogen concentrations in the water column and in the root zone. However, other plants in nitrogen-rich environments can obtain enough nitrogen through the roots for high growth rates. On the other hand, if water column ammonium or nitrate concentrations were sufficiently high or if nitrogen was available from nitrogen fixation (McRoy and McMillan 1977), the plants in low-nitrogen sediments could maintain maximum growth by utilizing both leaf and root uptake.

### CONCLUSIONS

Eelgrass leaves exhibit concentration-dependent uptake of both ammonium and nitrate for short term experiments at ambient nitrogen concentrations in the water column. However, ammonium is the preferred source of nitrogen with significantly higher short term uptake rates than nitrate. The proposed ammonium uptake system in eelgrass leaves allows increased accumulation when exposed to higher ammonium concentrations during tidal exchange and continuous uptake when ammonium concentrations are low.

Ammonium uptake by eelgrass roots is concentration dependent.

The ammonium uptake rate of eelgrass roots did not influence the uptake by eelgrass leaves and vice versa.

Considering the combined leaf and root uptake of ammonium in comparison to rates of eelgrass plant production, it appears that eelgrass plants can use both sediment and water column nitrogen resources to attain maximum growth rates. Experimental evidence suggests that in areas of ammonium-rich sediments, nitrogen uptake supplies enough of this nutrient to allow high growth rates, whereas many other eelgrass beds have ammonium-poor sediments in which the supply of nitrogen limits growth.

## CHAPTER 5: THE RESPONSE OF THE INTERSTITIAL AMMONIUM POOL OF AN EELGRASS BED TO ENVIRONMENTAL PERTURBATIONS

### INTRODUCTION

A natural perturbation induced by temperature fluctuation in the early 1930s is considered responsible for the widespread destruction of nearly all the eelgrass along the Atlantic coast of Europe and North America (Rasmussen 1973). Since that time, and partly because of that perturbation, much has been learned about the structure and dynamics of the eelgrass ecosystem (McRoy and Helfferich 1978; Phillips and McRoy 1980).

In the past, small scale human-induced perturbations in eelgrass ecosystems have been used to examine change in plant communities due to imposed changes in environmental conditions. The effect of available light on eelgrass bed structure was examined by the construction of shade screens that altered irradiance reaching the plant surface (Burkholder and Doheny 1968; Short *et al.* 1974; Backman and Barilotti 1976; Dennison 1979). Together these perturbations illustrate the reduction in eelgrass leaf biomass, leaf length, and shoot density resulting from a decrease in light intensity.

Experimental perturbations of an eelgrass ecosystem were also used to assess the effect of increased nutrient levels. Rayment (1947) reported that introduction of nutrients to the overlying waters produced a stimulation of eelgrass growth. Addition of nutrient fertilizer to the surface sediment of an eelgrass bed increased eelgrass density, biomass, and shoot length (Orth 1977). Based on these perturbation

experiments, Orth (1977) suggested that eelgrass in the Chesapeake Bay area was nutrient limited.

Nutrient supplies for eelgrass growth are available in both seawater and the upper layers of the sediments (Chapter 2). The uptake of phosphorus by eelgrass leaves and roots was demonstrated using  $^{32}\text{P}$  labelled phosphate (McRoy and Barsdate 1970). Similarly, uptake of nitrogen by eelgrass roots and leaves was measured with  $^{15}\text{N}$  labelled ammonium and nitrate (McRoy and Goering 1974; Iizumi 1979; Chapter 4).

Ammonium,  $\text{NH}_4^+$ , is produced in anoxic sediments by the decomposition of organic matter, and accumulates in the interstitial water. In the highly reduced eelgrass sediments, ammonium is removed from the interstitial pool by diffusion into the thin oxidized sediment surface layer and the overlying water column, by uptake by eelgrass roots, by adsorption onto sediments, and by incorporation into bacterial cells. The adsorbed ammonium in the sediments is present in two forms: fixed and exchangeable, as described by Rosenfeld (1979). The fixed ammonium is adsorbed into the clay structure and its interaction with the interstitial water is negligible. However, the exchangeable ammonium is easily released by ion exchange and exceeds the amount present in the interstitial ammonium pool (Chapter 2). The amount of exchangeable ammonium is dependent on the organic content of the sediment and on the sediment type, and can equilibrate with the interstitial pool in less than two hours under certain conditions (Rosenfeld 1979).

The objective of this research was to examine the removal of ammonium from the interstitial water by eelgrass root uptake and to assess the interaction of the plants with the interstitial pool. The

studies include four perturbation experiments: (1) a natural environmental perturbation in which an eelgrass bed was destroyed by ice damage (scouring) and the interstitial ammonium pool monitored during eelgrass colonization; (2) a perturbation introducing foreign substrate, with interstitial ammonium change monitored during colonization; and (3-4) two perturbations in which the effects of leaf removal and sediment isolation on the interstitial nutrient concentration were measured. The ammonium flux associated with the sediment interstitial pool was calculated from the ammonium regeneration measured in perturbations 3 and 4. The rates of eelgrass root uptake for ammonium and phosphate were also calculated from these perturbation experiments.

#### MATERIALS AND METHODS

These experimental studies were part of an investigation of the nitrogen requirements of eelgrass and the plants' utilization of available ammonium resources. The studies were carried out in Izembek Lagoon, located on the north side of the Alaska Peninsula (Fig. 2.1). The eelgrass meadows in this lagoon represent one of the most extensive stands of eelgrass, *Zostera marina*, in the world. The specific study site was an intertidal eelgrass bed located north of Grant Point where the mean depth at high tide was 0.7 m.

Eelgrass is distributed over a large area of the lagoon, forming vast meadows of non-homogeneous eelgrass density. Each extensive meadow is divisible into small homogeneous areas referred to as beds. Recognizing these eelgrass beds of relatively uniform plant character and nutrient condition reduces the problems of sampling.



The samples of eelgrass leaf material were collected with a  $1/16 \text{ m}^2$  quadrant, while for rhizome and root material a 16 cm diameter core sampler was used. Measurements of shoot density were made by counting leaf samples and by *in situ* counts in the experimental areas. Plant biomass samples were washed free of sediments in the field and dried to a constant weight at  $90^\circ\text{C}$  for 24 hr.

The following methods for sediment interstitial nutrient analysis were used for all the eelgrass perturbation experiments. Interstitial nutrient profiles were determined from replicate 4.7 cm diameter core samples manually collected from the experiment sites. The core samples were sliced into 5 cm sections directly into a sediment squeezer (Reeburgh 1967) and the interstitial water was filtered through a glass fiber filter into a sealed "Vacutainer". Samples for ammonium analysis were diluted 1:10 and analyzed colorimetrically (Koroleff 1976). Phosphate concentrations were also measured in the interstitial water samples (Strickland and Parsons 1972). The estimates of the interstitial ammonium pool in the sediments were determined by integrating the measured quantity of ammonium for each section to a depth of 15 cm. This calculation provided an estimate of the total amount of dissolved ammonium available to the plants per unit area of bottom. The fraction of organic matter in the squeezed sediment core samples was calculated by dividing the dry weight into the ash-free dry weight after combusting the samples for 24 hr at  $500^\circ\text{C}$ .

## Perturbation Experiments

The perturbed experimental areas were sampled for interstitial nutrients using sediment core samplers as described above. Leaf removal experiments consisted of a  $1/4 \text{ m}^2$  portion of an eelgrass bed in which all the leaves were clipped below the meristem. The sediment isolation experiment consisted of an equal area of substrate within this eelgrass bed that was clipped free of plants and sealed with a steel barrel lid. In both cases a control plot within the same eelgrass bed was marked for sampling so that the extent of change in nutrient pools could be measured.

Colonization studies were designed to investigate the response of the interstitial ammonium pool to the invasion and growth of eelgrass in unvegetated marine substrate. This experimental area (ca 1 m wide and 30 m long) was created by ice gouging during the severe winter of 1974-75 and was monitored each summer for four ice-free years starting in 1976. This scour probably resulted from the folding of an ice sheet which then gouged the lagoon bottom, scraping off the upper 3-5 cm layer of sediment. The gouging completely disrupted the eelgrass bed, removing all the leaves and rhizomes. The ice scour made a large area of substrate available for eelgrass colonization by both vegetative growth from adjacent beds and by seed germination. Three  $1/4 \text{ m}^2$  areas of the ice scour were marked off with cylindrical collars extending from the surface to 20 cm into the sediment, providing a permanent area for sampling during successive years (1976-79). The effect of sediment type on colonization was examined by establishing areas ( $1/4 \text{ m}^2$ ) of beach sand and of organic-rich terrestrial soil within the organic-rich scour area.

## RESULTS

Interstitial dissolved ammonium profiles in undisturbed eelgrass were characterized by depleted ammonium in the upper 10 to 15 cm zone, as a result of uptake by eelgrass roots (Fig. 2.4). The differences between these ammonium profiles represent typical spatial variation at most stations. Seasonal and diurnal variations were observed in the ammonium profiles relating to plant activity (Chapter 2); however, they do not substantially affect these results.

### Colonization

The ice scoured area was colonized during the second summer, 1976, by both vegetative growth and seedlings. Seeds from the previous year had germinated by mid-June, but the vegetative invasion from the bordering eelgrass bed did not begin until July. Little evidence of revegetation was seen until the third summer after the ice scour; the area had nearly recovered by the fourth summer (Fig. 5.1a).

A change in the size of the interstitial ammonium pool was evident through the years. The interstitial ammonium profiles from the ice scour area show high concentrations in the second summer and reduced levels during subsequent years coinciding with an increase in eelgrass density (Fig. 5.1a). The change in this interstitial ammonium pool during eelgrass colonization corresponds to the shoot density-ammonium concentration relationship described in Chapter 4. The ammonium pool size in the ice scoured area was high before eelgrass was present; after the second year of eelgrass colonization the relationship between shoot

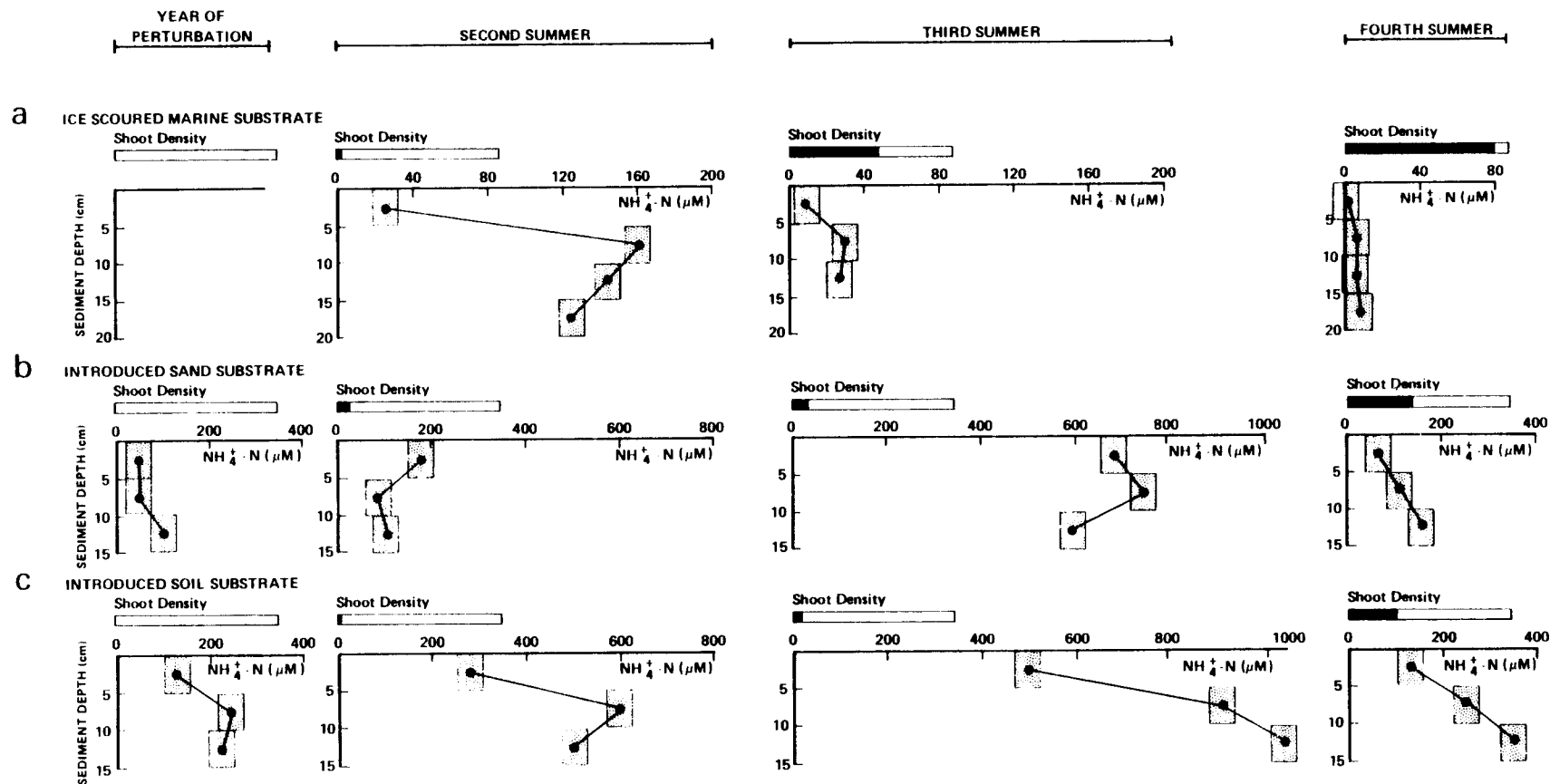


Figure 5.1. Three colonization experiments showing profiles of interstitial ammonium are presented with observed eelgrass shoot densities (maximum density = 1670 shoots per  $\text{m}^2$  of the bordering eelgrass bed). The shaded blocks indicate the sediment section that is represented by the plotted concentration: (a) Ice scour perturbation of high organic marine substrate; (b) Introduced substrate of low organic beach sand; (c) Introduced substrate of high organic non-marine soil.

density and the ammonium pool was similar to that found in undisturbed eelgrass beds (Fig. 5.2).

Experiments designed to examine the extent of colonization in different types of foreign substrate indicated a slower revegetation but much higher ammonium concentrations than were observed in the natural highly organic marine sediment (5.3% organic content; Fig. 5.1a). Seedling abundance for the second and third summers was low in the foreign substrate, with 110 seedlings  $\text{m}^{-2}$  in sand and 54 seedlings  $\text{m}^{-2}$  in soil, compared to an average density in Izembek Lagoon of 400 seedlings  $\text{m}^{-2}$ .

The concentration of ammonium in these foreign substrates was greater the second summer than the first and still greater by the third summer (Fig. 5.1b, c). The fourth summer, the increased eelgrass shoot density was accompanied by a decrease in the ammonium concentrations. The greater interstitial ammonium pool for the second and third summers, evident in both the sand (0.9% organic content) and soil (5.8% organic content) substrate (Fig. 5.1), was not accompanied by a change in the sediment organic content.

#### Leaf Removal and Sediment Isolation

The results of these experiments are expressed as the difference in ammonium concentrations ( $\Delta \text{NH}_4^+$ ) between the experimental sampling area and the control area (Fig. 5.3 and 5.4). The leaf removal experiment and the control at Station S (mud substrate, 5.0% organic content) in July of 1977 showed variation in interstitial ammonium concentrations ( $\Delta \text{NH}_4^+$ ) at the initial clipping (Day 0). But a larger  $\Delta \text{NH}_4^+$  was

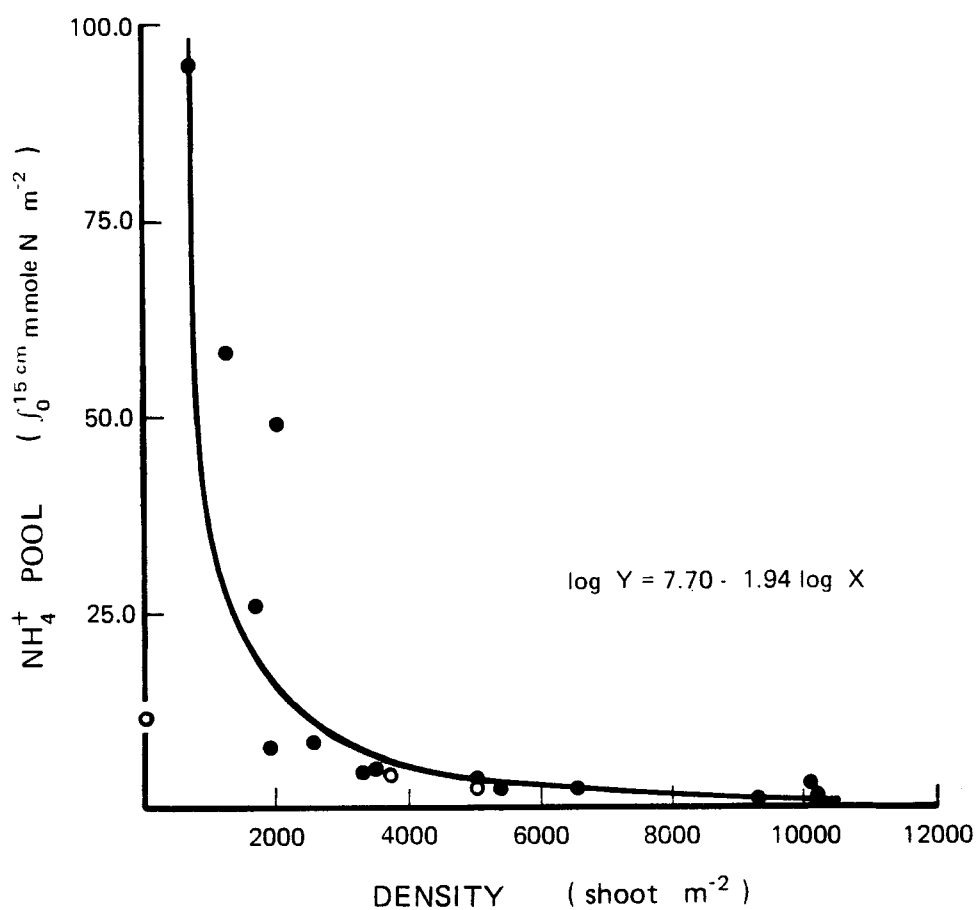


Figure 5.2. Shoot density vs. integrated interstitial ammonium (0-15 cm). Undisturbed eelgrass beds (●) and colonization samples (○) in an ice scour from 1976, 1977, and 1978, indicating increasing density. Logarithmic transformation of density and ammonium indicating a correlation coefficient of 0.97 and the calculated regression line and equation (replotted from Fig. 3.2).

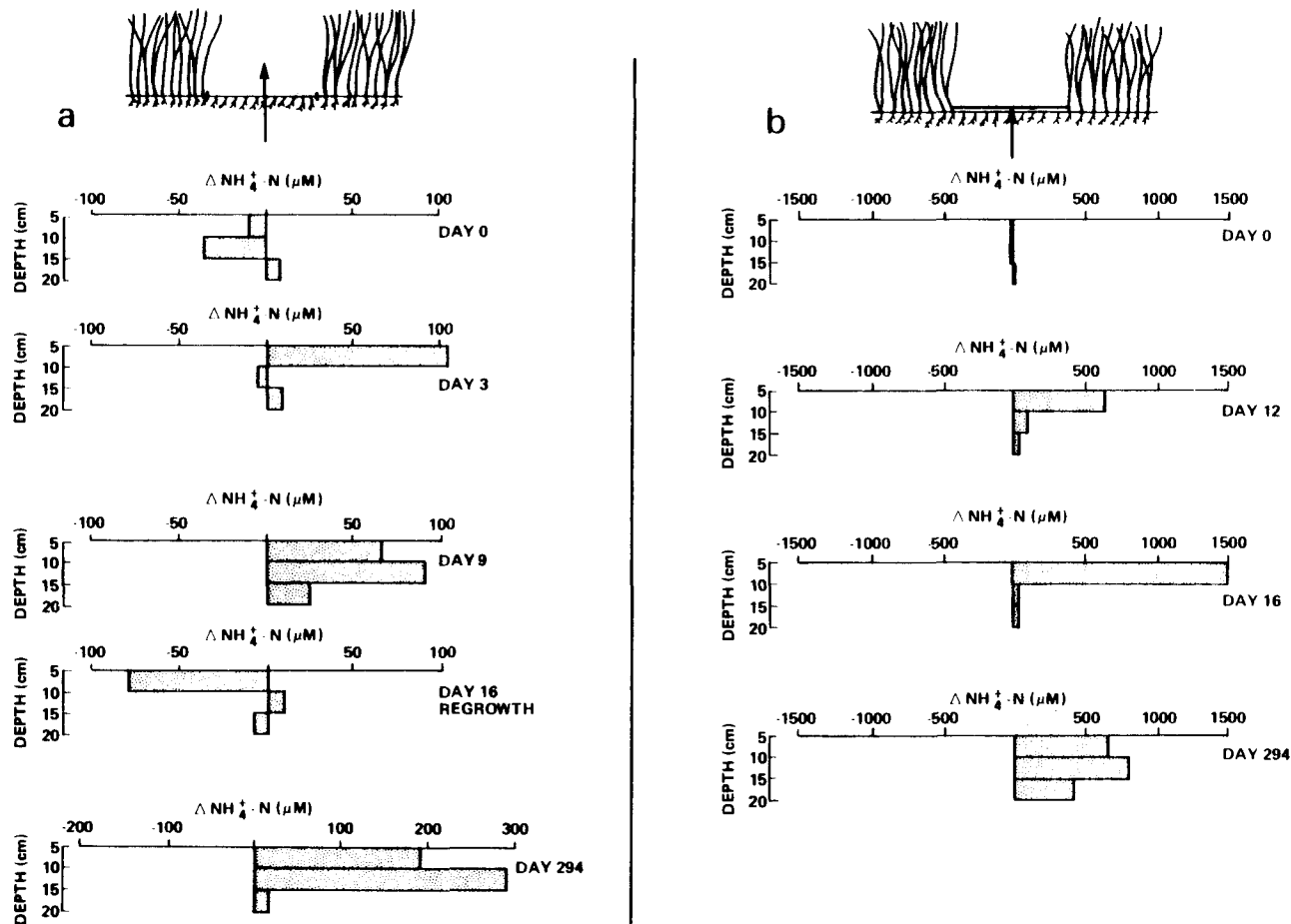


Figure 5.3. Leaf removal and sediment isolation experiments. Ammonium profiles vs. depth plotted as the difference between the experimental conditions and a control ( $\Delta \text{NH}_4^+$ ). Day 0 indicates the natural variation between experimental area and control. Experiment at Station S Izembek Lagoon initiated July 21, 1977: (a) Leaf removal experiment allowing flux from the sediment. Regrowth of eelgrass was observed on Day 16 but the following summer, Day 294, no eelgrass was evident; (b) Sediment isolation experiment sealing the sediment surface preventing nutrient flux.

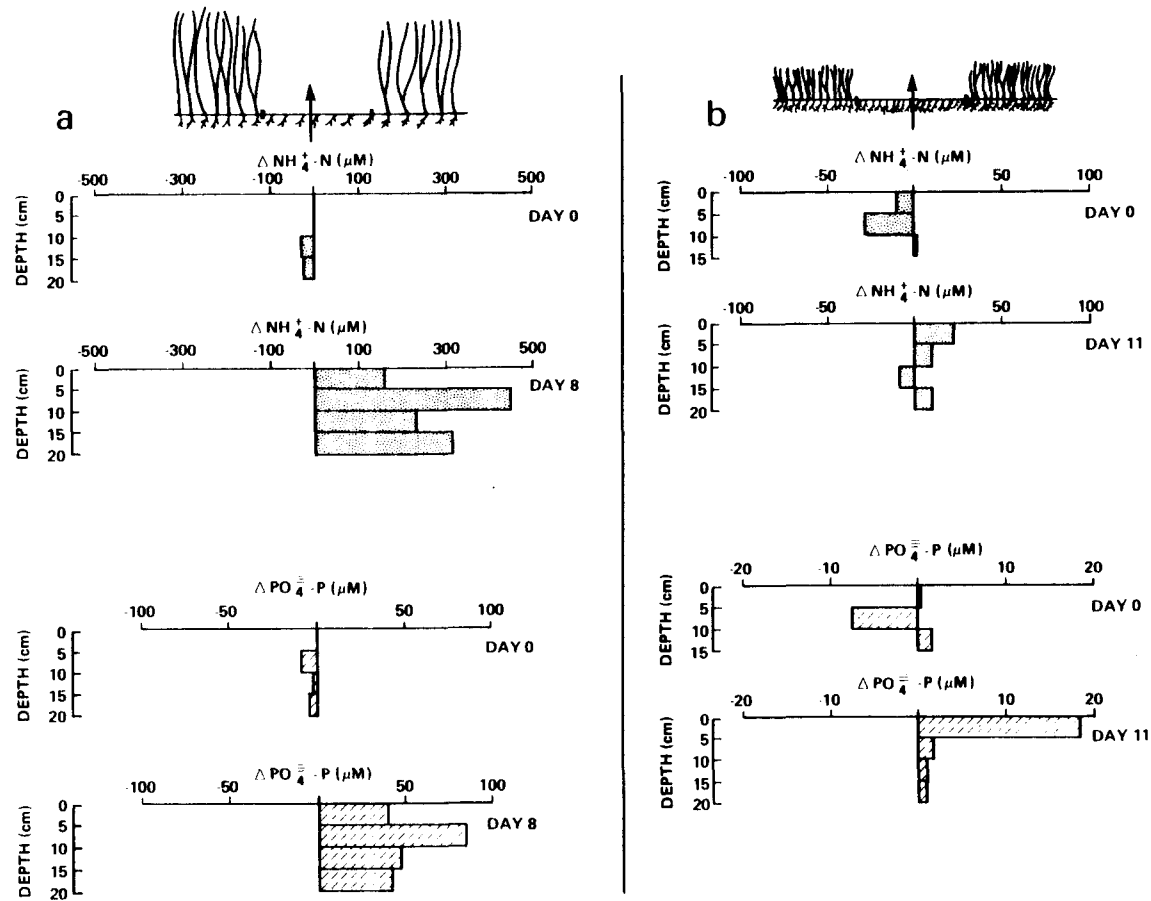


Figure 5.4. Leaf removal experiment allowing flux from the sediments. Ammonium ( $\Delta \text{NH}_4^+$ ) and phosphate ( $\Delta \text{PO}_4^{3-}$ ) profiles plotted as the experimental conditions minus a control. Day 0 indicates natural variation between experimental area and control. Initiated June 4, 1978 in Izembek Lagoon: (a) High organic sediment and low eelgrass shoot density; Station 9; (b) Low organic sediment and high eelgrass shoot density; Station 4.



evident after the leaf removal (Fig. 5.3a). Three days after the leaf removal, an increase in ammonium concentration was evident in the upper 5 cm, while at Day 9 the increased concentration was obvious in the entire 15 cm section. Eelgrass regrowth was observed on Day 16 and the ammonium concentration in the experimental area was low, resulting in negative values for  $\Delta \text{NH}_4^+$ . The eelgrass did not survive the winter in the experimental area and the following summer, 294 days after the leaf removal with no sign of regrowth evident, ammonium concentrations greater than those of the control plot ( $\Delta \text{NH}_4^+$ ) were observed. The rate of accumulation of ammonium in the sediments between 3 days and 9 days after plant removal was calculated to be  $65 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$ .

Ammonium regeneration and desorption were monitored at Station S by sealing the sediment surface to prevent any vertical diffusion across the sediment-water interface. The ammonium concentrations were much higher than in the leaf removal experiment throughout the same 16 day period (Fig. 5.3b). The following summer the surface was still sealed, and the elevated concentrations were more uniformly distributed over the upper 15 cm (Fig. 5.3b). The calculated ammonium increase for the period from Day 12 to Day 16 is  $300 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$ . Ammonium diffusion was calculated by difference between the sealed surface experiments and the leaf removal experiments, indicating a diffusion rate of  $235 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$ .

Experiments were conducted during the period of maximum plant growth in June 1978 to estimate the greatest removal rate of both ammonium and phosphate from the sediments. This net root uptake rate was

calculated from the rates of accumulation of interstitial ammonium and phosphate, assuming constant diffusion before and after leaf removal. These eelgrass removal experiments were carried out at two stations of different sediment organic content. The calculated uptake rate for these experiments positively correlated with sediment organic content and with the size of the interstitial nutrient pools (Table 5.1). At Station 9, with an eelgrass biomass of  $1090 \text{ g m}^{-2}$  and 6.6% sediment organic matter, the calculated root uptake was  $450 \text{ } \mu\text{mole N m}^{-2} \text{ hr}^{-1}$  for the plant removal experiment (Fig. 5.4a), while at Station 4 (Fig. 5.4b), with a biomass of  $1770 \text{ g m}^{-2}$  and a much lower organic content (3.1%), the calculated uptake rate was  $3 \text{ } \mu\text{mole N m}^{-2} \text{ hr}^{-1}$ .

## DISCUSSION

The dissolved ammonium pool in the sediments is an important interactive part of an eelgrass bed. Interstitial nutrients are directly available to the plants through the root/rhizome system; however, nitrogen is also utilized from the water column (Chapters 2 and 3). Losses of ammonium from the interstitial pool are recovered by desorption from the sediments and microbial regeneration, but can they meet the demand for ammonium by eelgrass roots?

### Perturbation Effects

The colonization experiment shows eelgrass shoot density can modify the size of the dissolved interstitial ammonium pool (Fig. 5.1). During colonization the ammonium pool size decreased with increasing density in a manner that supports the relationship described in Fig. 5.2. Thus,

Table 5.1. Leaf removal experiment at two stations in Izembek Lagoon during June 1978 presenting the eelgrass standing stock and ammonium uptake rates by eelgrass roots calculated from the buildup of nitrogen and phosphate in the sediments.

Station	Shoot Density # m <sup>-2</sup>	Total Biomass g m <sup>-2</sup>	Sediment Organic %	Eelgrass Requirement*		Root Uptake		Leaf Uptake Requirement % of Total
				NH <sub>4</sub> <sup>+</sup> **	N:P	NH <sub>4</sub> <sup>+</sup> **	N:P	
9	2570	1090	6.6	1830	23:1	450	15:1	75
4	9308	1770	3.1	2970	23:1	3	1.2:1	99.9

\*Based on 0.31 mg C g(dry)<sup>-1</sup> hr<sup>-1</sup>.

\*\*μmole N m<sup>-2</sup> hr<sup>-1</sup>.

the ammonium pool size is modified by eelgrass revegetation; i.e., the pool size responds to changes in shoot density. Further evidence for the effect of shoot density on the ammonium pool size was provided by the leaf removal experiments in which increased ammonium was observed in the interstitial water 3 days after the growing leaves were clipped (Fig. 5.3a).

These two experimental cases, revegetation and devegetation, both demonstrate the dependence of ammonium on eelgrass density; that is, ammonium pool size was maintained at a lower concentration due to uptake by eelgrass roots.

Perturbation experiments on the nutrient pool in eelgrass beds (Orth 1977) indicated an increase in shoot (turion) density following enrichment with fertilizer at the sediment surface. This enrichment perturbation altered the eelgrass bed from a nutrient limited condition, and stimulated a plant response of new shoot production (Orth 1977). The response is the same in other vascular plants; nutrient enrichment of stressed plants causes rapid lateral shoot production (Chapter 4). Apparently the immediate reaction of the plant to a removal of nutrient stress is to initiate lateral branching of the rhizome. To obtain a good test of the relationship between density and the sediment ammonium pool in Fig. 5.2, a continuous enrichment experiment is necessary. Such an enrichment of the interstitial ammonium pool would, according to this hypothesis (Fig. 5.2), result in a decrease in density as the eelgrass bed stabilizes.

## Colonization

The colonization of marine substrate by eelgrass to its former density was completed only four years after a major natural perturbation had destroyed a portion of the eelgrass bed. The rapid regrowth was facilitated by an abundant available seed stock and an actively growing dense eelgrass bed bordering the disturbed area. Ammonium concentrations in these organic sediments were high the second year in the absence of eelgrass but were depleted the following years as the density increased (Fig. 5.1a). This colonization study supplies direct evidence of the relationship between eelgrass shoot density and the interstitial ammonium pool. The second summer after the ice had removed eelgrass from the area, there was little regrowth, and the interstitial ammonium concentrations were much higher than in the surrounding eelgrass bed. The ammonium pool during the second summer was large, about  $11.5 \text{ mmole N m}^{-2}$ , and displaced from the density ammonium regression (Fig. 5.2). However, by the third summer the smaller ammonium pool and increased shoot density shown in this eelgrass bed were similar to those of beds that were characterized by the density-ammonium relationship. The fourth summer, the still smaller ammonium pool and a density as high as the surrounding shoot density continued to follow this empirical relationship (Fig. 5.2). Thus, the colonization study of this eelgrass bed helped confirm the correlation between shoot density and the ammonium pool, and demonstrated that the growth of eelgrass can affect interstitial ammonium concentrations.

Eelgrass colonization of introduced foreign substrates was slower than in the area of natural marine sediment. However, there was little difference in colonization rate between the organic-poor sand substrate and the organic-rich soil substrate (Fig. 5.1b and c). Interstitial ammonium profiles in the sediments decreased after a substantial eelgrass density was established, but the ammonium concentrations were still much higher than in the marine substrate. Similarity between the high ammonium concentrations in the organic-poor sand substrate and the soil substrate were unexpected, due to the lack of particulate organic nutrient source, and remain unresolved.

#### Ammonium Flux

The genesis of ammonium in the interstitial water was assumed to result primarily from the decomposition of organic matter. In sediments associated with eelgrass, ammonium addition to the interstitial water was balanced primarily by removal through uptake by the roots and diffusion into the overlying water.

The regeneration and desorption of ammonium in these sediments and the flux of ammonium from the sediment was measured to estimate cycling through the interstitial pool. The experiments involving leaf removal provided time course measurements of interstitial ammonium, from which rates of ammonium removal by roots were calculated (Fig. 5.3a). This calculation does not allow for the increase in diffusion and adsorption with increased concentration, suggesting that the calculated ammonium uptake rates are underestimated. The sediment isolation experiment

was used to calculate the flux of ammonium through the interstitial pool (Fig. 5.3b). The rate of ammonium removal by the plants,  $65 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$ , in late July was much less than the total regenerated ammonium, giving, by difference, an estimate of diffusion of  $235 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$ . This ammonium diffusion rate is comparable to those measured in other marine sediments of  $-4$  to  $276 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$  (Hale 1976) and up to  $400 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$  (Nixon *et al.* 1976).

The rates of both ammonium and phosphate removal during the summer maximum growth period were used to assess nutrient uptake by roots of active growing plants (Fig. 5.4). The calculated ammonium and phosphate uptake by roots was greater in the highly organic substrate than in the sandy organic-poor substrate. These uptake rates probably represent underestimates for ammonium and phosphate resulting from adsorption on the sediments. The highest uptake rate by roots was measured in mid-summer at Station 9 with 6.6% organic matter. The ammonium uptake by eelgrass roots was estimated to be  $450 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$ , and the phosphate uptake rate was estimated to be  $30 \mu\text{mole P m}^{-2} \text{ hr}^{-1}$  for this eight-day leaf-removal experiment (Table 5.1). The N:P ratio for uptake was 15:1 compared to a plant composition N:P = 23:1 (McRoy 1966) indicating that the nitrogen requirement could be satisfied if phosphate were taken up from the sediments in excess. Surplus phosphate uptake by roots and leakage from leaves into surrounding water was previously demonstrated by McRoy and Barsdate (1970).

The uptake rates estimated for organic-poor substrate (3.1% organic matter) were  $3.0 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$  for ammonium and  $2.5 \mu\text{mole P m}^{-2}$

$\text{hr}^{-1}$  for phosphate at Station 4 (Table 5.1). The N:P ratio for these organic-poor sediments is 1.2:1, and the low nutrient concentrations indicate the lack of ammonium in the interstitial water and possibly insufficient nitrogen available for plant growth. Thus, the possibility of nitrogen limitation is evident in sediments of low organic matter.

### CONCLUSIONS

Perturbation experiments provide a successful mechanism for the study of certain ecosystem processes and responses. The use of both human induced and natural perturbations is valuable in portraying the interaction of interstitial ammonium concentrations and eelgrass colonization. The rate of colonization was found not to rely on sediment ammonium concentrations alone. Data from these colonization experiments support the logarithmic relationship between eelgrass shoot density and the interstitial ammonium pool size.

The rates of ammonium flux in and out of the interstitial waters were evaluated from the results of the leaf removal and sediment isolation experiments, illustrating a useful method for future studies of nutrient exchange. Finally, these studies provide estimates for ammonium regeneration and diffusion, and uptake of ammonium by eelgrass roots. The ratio of nitrogen to phosphorus uptake relative to the plant requirement demonstrates the variation between different eelgrass beds and suggests that some beds are limited by nitrogen.



## CHAPTER 6: SIMULATION OF NITROGEN UTILIZATION IN EELGRASS MEADOWS

### INTRODUCTION

Mathematical modelling in marine environments has developed from basic formulation of plankton populations to interactive descriptions of organism physiology and complex ecosystem analysis (Kremer and Nixon 1978). Several modelling studies have investigated aspects of marine macrophytes and ecosystem function, including: analysis of kelp growth (North 1967); oxygen metabolism in a salt marsh (Nixon and Oviatt 1973); salt marsh nutrient flux (Pomeroy *et al.* 1972); salt marsh ecosystem simulation (Hopkinson and Day 1977; Weigart 1979); and seagrass production analysis (Short 1980). Simulation of nitrogen utilization in a salt marsh ecosystem suggests that nitrogen levels in the soil are depleted by plant uptake and bacterial immobilization (Hopkinson and Day 1977). However, Hopkinson and Day's general model does not examine the methods and sources of nitrogen acquisition by the plants. The modelling study presented in this chapter is designed to investigate specific aspects of nitrogen utilization by eelgrass plants and the importance of nitrogen resources in the ecosystem to plant growth.

The value derived from the development of an ecological model in this eelgrass study is three-fold. First, it creates a network that allows numerical evaluation of biological information about the plant. This analysis requires examination of experimentally determined physiological relationships, in conjunction with empirical observations of the environment and the plant ecosystem. Second, the formulation of interactive relationships between ecosystem components requires a look

at the discrete parts of the plant ecosystem. Finally, the development of the interactive network of mathematical formulations demonstrates weaknesses in the model construction and in the observational data.

Simulation is a mechanism for evaluating the observed interaction between various components of the system; unlike the natural ecosystem, all the dynamic interactions are known. Comparison of simulated rates and stock sizes with empirical observations provides a test of the interactive network and the functional relationships within the model. Simulation analysis also provides a facility for hypothesis testing and prediction, an ultimate goal of ecology.

#### MODELLING METHODS

A numerical model of eelgrass production (Short 1975) was adapted to the environmental conditions of Izembek Lagoon, Alaska in a simplified form; streamlining of the model involved eliminating calculation of individual leaf production in favor of shoot growth. Additionally, the effect of current speed on plant growth was removed in view of recent findings refuting this relationship (Fonseca and Thayer 1979). In light of the studies on nitrogen resources in eelgrass (Chapters 2-5), it is obvious that nitrogen availability is largely responsible for the patterns of growth previously ascribed to current effects. The influences of current flow on the distribution of nutrient resources have not been quantitatively examined, but field observation indicates a direct association.

The model, based on observed environmental conditions and empirical relationships for plant production and death, simulates seasonal

growth of eelgrass and calculates numerous standing stock characteristics (Short 1975, 1980). The required environmental data for model simulation include seasonal temperature, irradiance, and wind (Fig. 6.1) in addition to initial conditions (Table 6.1) of leaf and root biomass, leaf length and width, and a seasonal density function. Shoot density is fit with a truncated sine function and used as a forcing function in the model. Leaf length is calculated from the leaf biomass data and an empirical ratio of the average length of a full grown leaf to the leaf weight. The ratio of weight to length was established for each station as part of the initial conditions (Table 6.1).

A simplified conceptual model for eelgrass growth illustrates the major interactive components that are involved in nitrogen utilization (Fig. 6.2). In this model the photosynthetic activity and carbon uptake are determined by light, temperature, and the nitrogen available to the leaves and roots. The large ammonium pool in eelgrass sediments is a major source of nitrogen, although the smaller water column nitrogen concentrations continually flowing by the leaves can supply a significant part of the plant's nitrogen requirement (Chapter 4). The rates of uptake from the sediments and water column are based on hourly rates evaluated over 24 hr, a calculation producing a maximum daily nitrogen uptake rate (Chapter 4). The nitrogen resources seasonally available to eelgrass through the leaves and roots were described earlier (Chapter 2) and were fit with a mathematical function appropriate to the data for use in simulation (Fig. 6.3). These mathematical formulations and the derived equations for nitrogen uptake have been

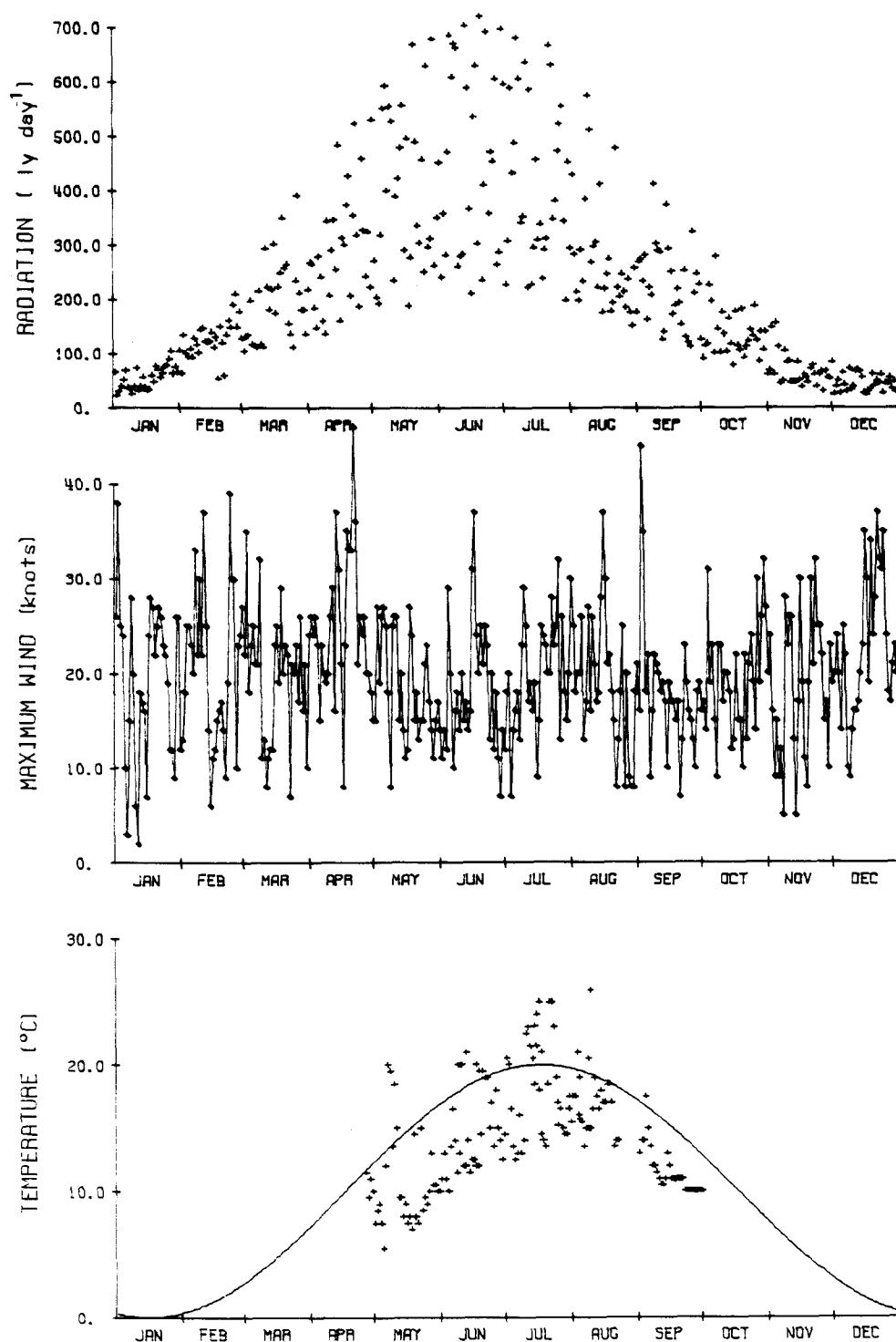


Figure 6.1. Daily environmental conditions for Izembek Lagoon: (a) Radiation calculated from the theoretical equations for maximum surface radiation and a stochastic cloud cover model (Appendix B); (b) Maximum observed wind speed sustained over a three hour period at Cold Bay Airport (National Weather Service, Local Climatological Data 1970); (c) Maximum temperatures for 1967 (McRoy unpublished) and theoretical curve.

Table 6.1. Initial conditions used in the simulation of eelgrass beds in Izembek Lagoon, Alaska.\* Station S was used for the calibration.

Stations	S	14	9	8	4	2	1
Month	Aug	Aug	Aug	Aug	Aug	Aug	June
Day	12	1	12	12	1	12	1
Mid-tide depth (m)	1.3	2.0	0.8	0.8	0.3	0.3	0.3
Leaf length (m)	0.67	1.49	1.24	1.28	0.33	0.70	0.19
Leaf width (cm)	0.23	0.36	0.28	0.21	0.17	0.16	0.15
Leaf biomass ( $\text{g m}^{-2}$ )	450	268	664	479	394	254	137
Root biomass ( $\text{g m}^{-2}$ )	532	719	722	290	527	500	420
Number of leaves (# shoot <sup>-1</sup> )	3.0	3.6	3.7	3.3	3.0	3.0	3.0
Yearly maximum shoot <sub>2</sub> density (# m <sup>-2</sup> )	4600	1748	2656	5000	9988	9500	6560
Ratio dry wt to length (g m)	0.18	0.29	0.27	0.14	0.09	0.10	0.11

\* Data from McRoy and Klug (unpublished); this study.

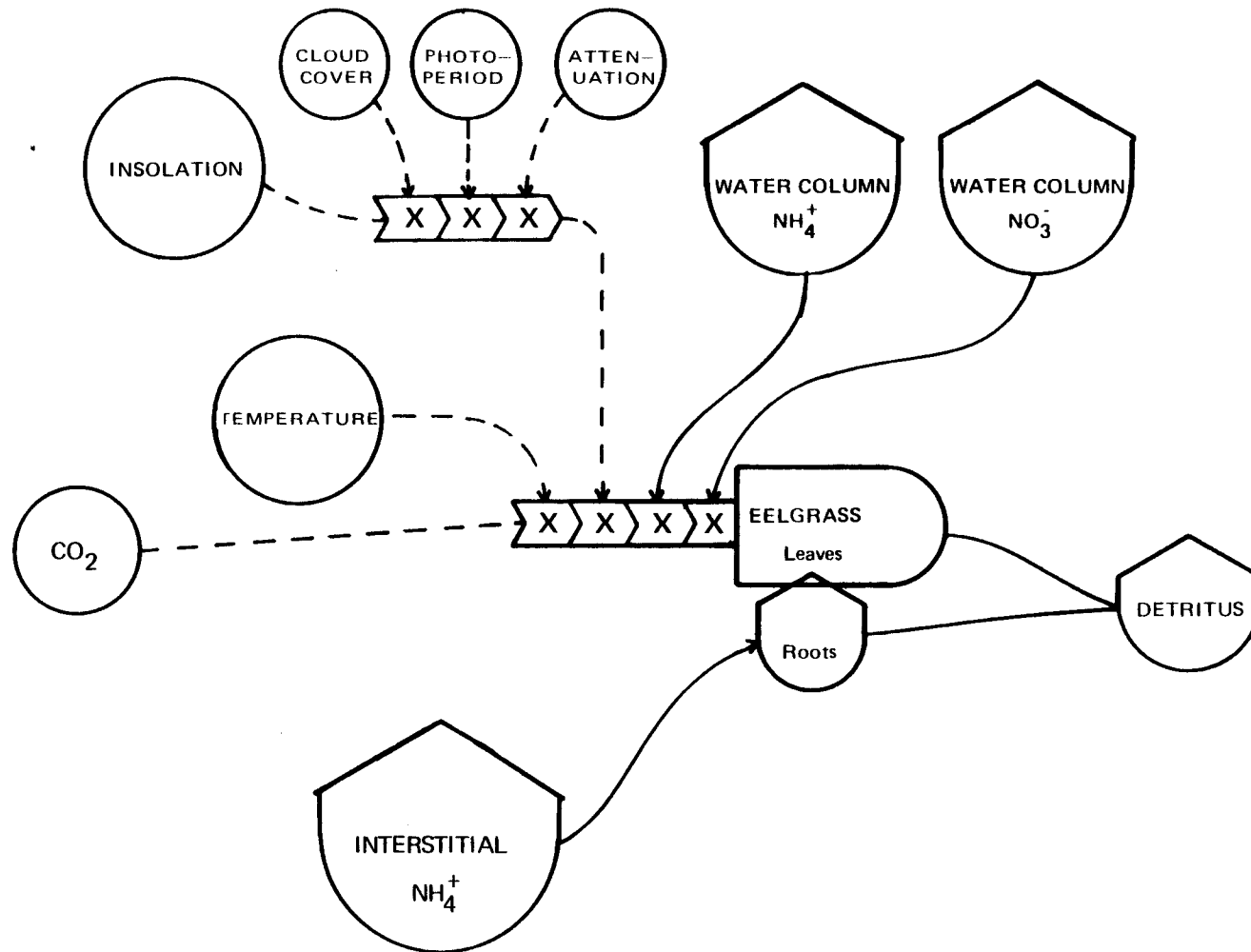


Figure 6.2. Conceptual diagram of nitrogen utilization by eelgrass as described in the computer simulation. The rate of nitrogen uptake into leaf or root material and the solar energy input control the flow of carbon. Solid lines represent the flow of nitrogen through the system; dashed lines are carbon and energy interactions.

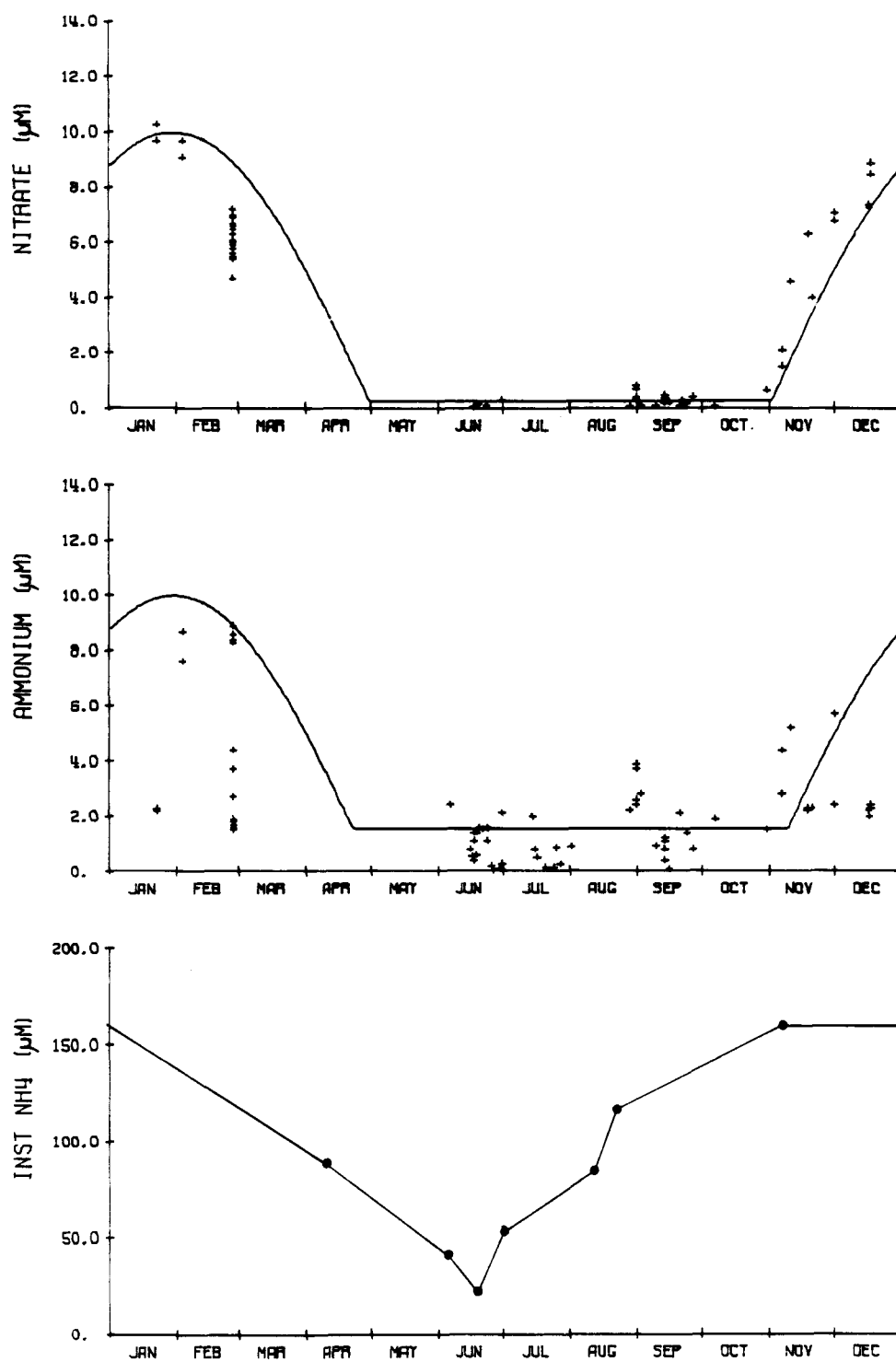


Figure 6.3. Model formulation with observed data (Fig. 2.3) for the water column concentrations of ammonium and nitrate, and interstitial ammonium concentration used in the eelgrass simulation.

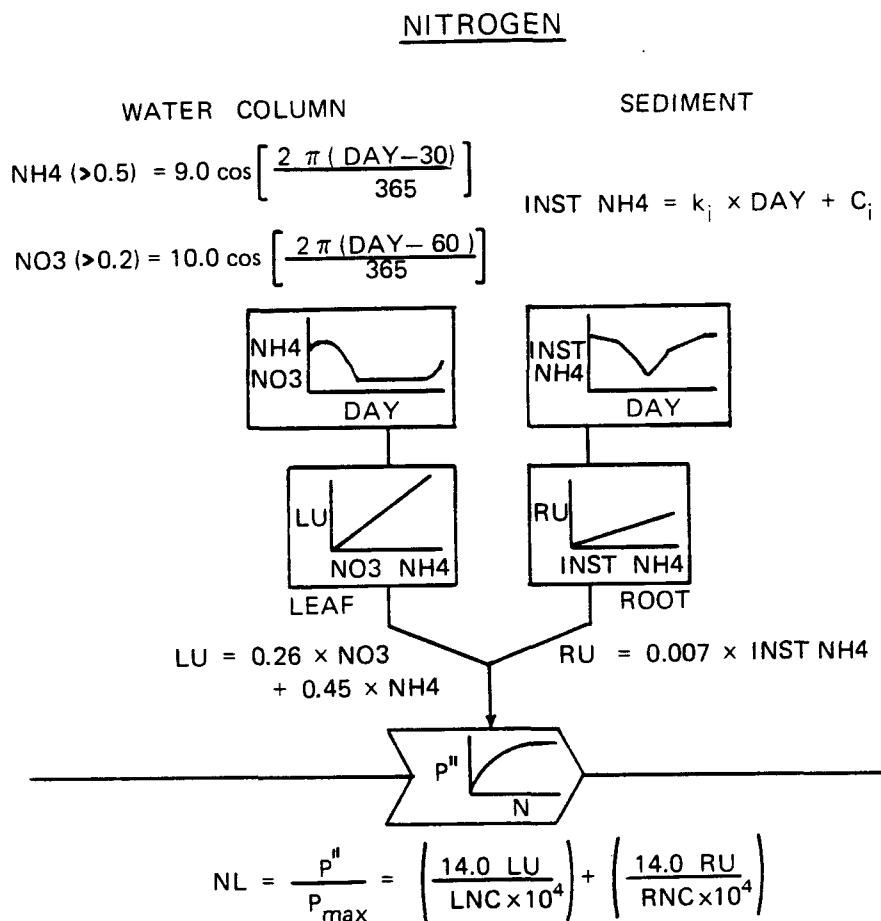


Figure 6.4. Diagram of the mathematical formulation for nitrogen utilization in the eelgrass simulation model. The equations for the seasonal nitrogen resources (Fig. 6.3); leaf (LU) and root (RU) uptake equations derived from the kinetic experiments (Chapter 4); leaf nitrogen content (LNC) of 2.4% and root nitrogen content (RNC) of 1.7% N; the nitrogen limitation (NL) equation based on the available nitrogen and the light determined production rate ( $P_{\max}$ ).



combined in an equation diagram showing the major components that control eelgrass growth in the model (Fig. 6.4).

Several assumptions implicit in this formulation of the nitrogen model need to be mentioned. First, nitrate and ammonium are assumed to be taken up simultaneously and at independent rates since no studies are known concerning inhibition of uptake by one ion or the other at water column concentrations. Also root and leaf uptake rates are independently formulated, reflecting experimental work (Chapter 4). The nitrogen content of the plant is assumed constant during the year and throughout the leaves (2.4% of dry weight) and the roots (1.7% of dry weight). Although wide variations in the seasonal nitrogen composition and in the nitrogen content within a plant have been reported (Harrison and Mann 1975; Aioi and Mukai 1980), this simplifying assumption is necessary since the influence of nitrogen supply on nitrogen content and the range of variation of nitrogen content in Izembek Lagoon are unknown. The assumption of constant plant nitrogen is tested with the model by running consecutive simulations with observed plant nitrogen composition (Page 103). Finally, the eelgrass plants in the model do not store nitrogen in their tissues; thus, any nitrogen taken up and not needed in metabolism is lost from the plant.

## THE MODEL

### Model Calibration

Before applying the growth model to eelgrass beds of various environmental conditions, initial "fine-tuning" of the model for one selected location was necessary. Station S, located north of Grant Point in

Izembek Lagoon (Fig. 2.1), was chosen because of the available data on seasonal sediment ammonium concentrations (Fig. 2.4) and seasonal biomass (Fig. 6.4). Also, nitrogen uptake and regeneration measurements were available for this station (Chapter 5).

The initial conditions for the plant community and the local environment were established in the computer model for Station S (Table 6.1). Simulations were run to calibrate the model coefficients and obtain a reasonable fit to the observed data (Fig. 6.5). The leaf dry weight per shoot was important in the model because leaf biomass on an area basis is influenced by the forcing function for plant density. Leaf length calculation is also presented for comparison to observed leaf length data.

#### Modelling Nitrogen Utilization

Nitrogen utilization is formulated so that the daily eelgrass growth rate is restricted when insufficient nitrogen is available to form tissue of a specific nitrogen content. That is, growth in the model continues until the nitrogen taken up through the leaves and roots is exhausted. The growth equation ensures that daily variation in light-controlled leaf growth is suppressed when nitrogen limitation is dominant. This is illustrated in the simulation of Station S where nitrogen limited growth occurs from early May through most of October (Fig. 6.6a). The variation in the slope of the growth curves in summer results from forced changes in the available nitrogen (Fig. 6.3). The reduction of growth in summer results primarily from depletion of the sediment ammonium as uptake by roots exceeds the supply of nitrogen

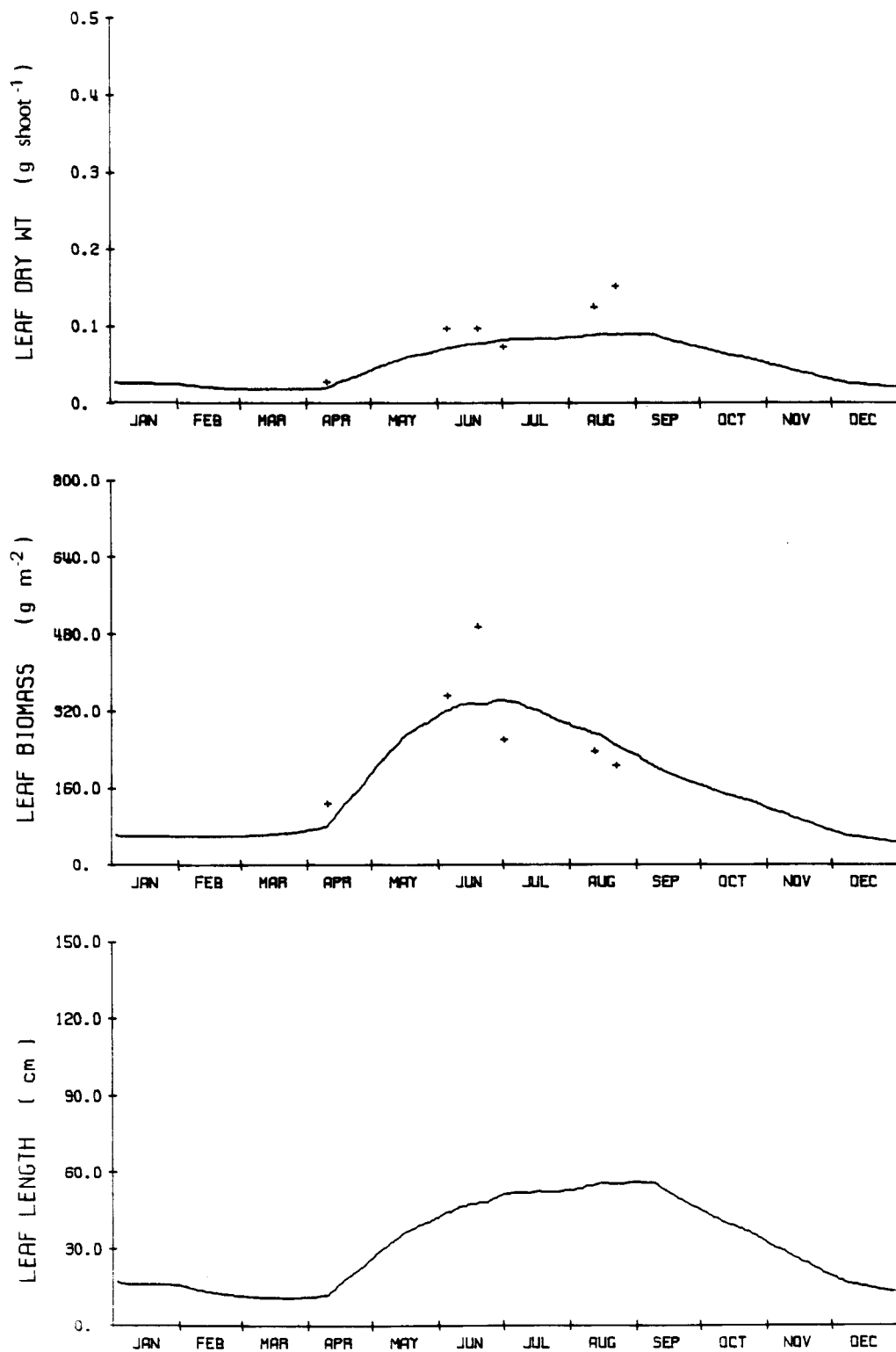


Figure 6.5. Simulated (-) and observed (+) data for eelgrass leaf dry weight per shoot, leaf biomass m<sup>-2</sup>, and leaf length at Station S (Data collected between May 1976 and July 1978).

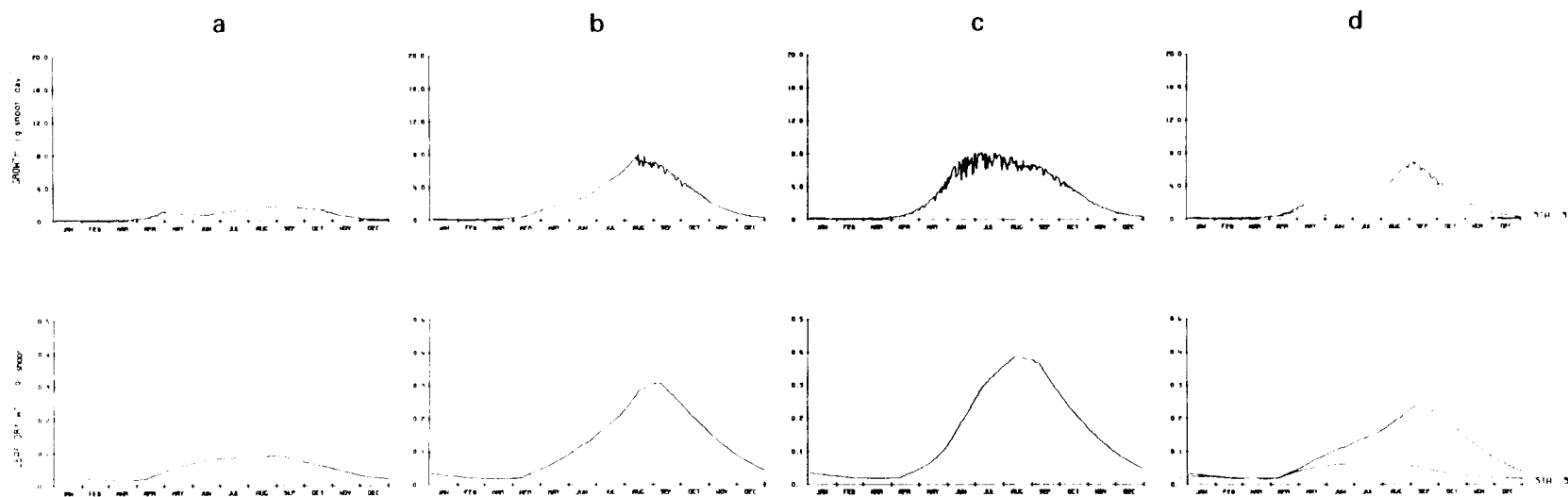


Figure 6.6. Simulated data for eelgrass leaf growth and leaf dry weight at Station S: (a) Standard run with initial conditions as specified in Table 6.1; (b) Experimental run with  $4.0 \mu\text{M}$  ammonium added to the water column each day; (c) Experimental run with excess nitrogen available to the leaves and roots; (d) Experimental run with maximum (lower line) and minimum (upper line) plant nitrogen content in the leaves and roots of eelgrass.

to the sediment pool (Chapter 2). However, leaf uptake from the water column can have a substantial effect on eelgrass growth. An increase in the ammonium concentration of the water column to  $4.0 \mu\text{M}$  ammonium produces a substantial increase in plant biomass and a reduction in nitrogen limited growth from the end of July throughout the year (Fig. 6.6b). This reduction in nitrogen limitation was suggested earlier in the analysis of whole plant uptake kinetics (Fig. 4.5).

The impact of nitrogen limitation on eelgrass growth at Station S is addressed in the simulation model by flooding the sediments and water column with ammonium and nitrate. The results demonstrate an increase in simulated leaf dry weight compared to the observed leaf dry weight (Fig. 6.6c). This removal of nitrogen limitation produces light dominated growth rates throughout the year, illustrated by the erratic variation in shoot growth rate. The simulation supplying excess nitrogen to Station S shows that nitrogen effects on growth are relatively unimportant in the early spring but do strongly affect the maximum attainable eelgrass biomass.

The influence of nitrogen availability on plant growth can be manifested in the nitrogen content of the plants; high nitrogen environments promote plant tissue rich in nitrogen and areas of low nitrogen produce nitrogen-depleted plants. Seasonal and spatial variation are restricted in the standard simulations. However, the influence of a varying nitrogen composition in the plants has been tested in the model by simulating the range of observed data for eelgrass (Aioi and Mukai 1980). These simulations (Fig. 6.6d) demonstrate the range in attainable eelgrass biomass resulting from a minimum nitrogen content of 1.5% of dry weight

in the leaves and 1.2% in the roots and a maximum of 3.4% in the leaves and 1.9% in the roots. Simulation with maximum nitrogen composition for these plants has only a small effect on the leaf biomass at this station. However, plants with low nitrogen composition produce greater leaf biomass in the fall.

#### Simulation of a Transect

The variation in plant biomass and morphology across an eelgrass meadow (Chapters 2 and 3) provides a useful test of the simulation ability of the eelgrass model to predict the pattern of standing stock across a range of environmental conditions. Additionally, simulation of eelgrass beds having different light and nutrient conditions enables an examination of nitrogen limitation.

The computer model calibrated for Station S was fit with initial conditions (Table 6.1) appropriate for each of the stations along a transect (Fig. 2.1). To test this model effectively the initial conditions for a number of stations were simulated and the model predictions of biomass data were compared to empirical data. These simulations were run with appropriate sediment nitrogen concentrations (Table 2.3) for each of the transect stations, and the simulated standing stock data calculated for each day was plotted with field data (Figs. 6.7 to 6.12). The leaf standing stock data compared to the model results represents all available data for the 1978 field season including leaf dry weight per shoot and length measurements from Dennison (1979) and leaf biomass data (McRoy unpublished). The variation in the observed leaf biomass

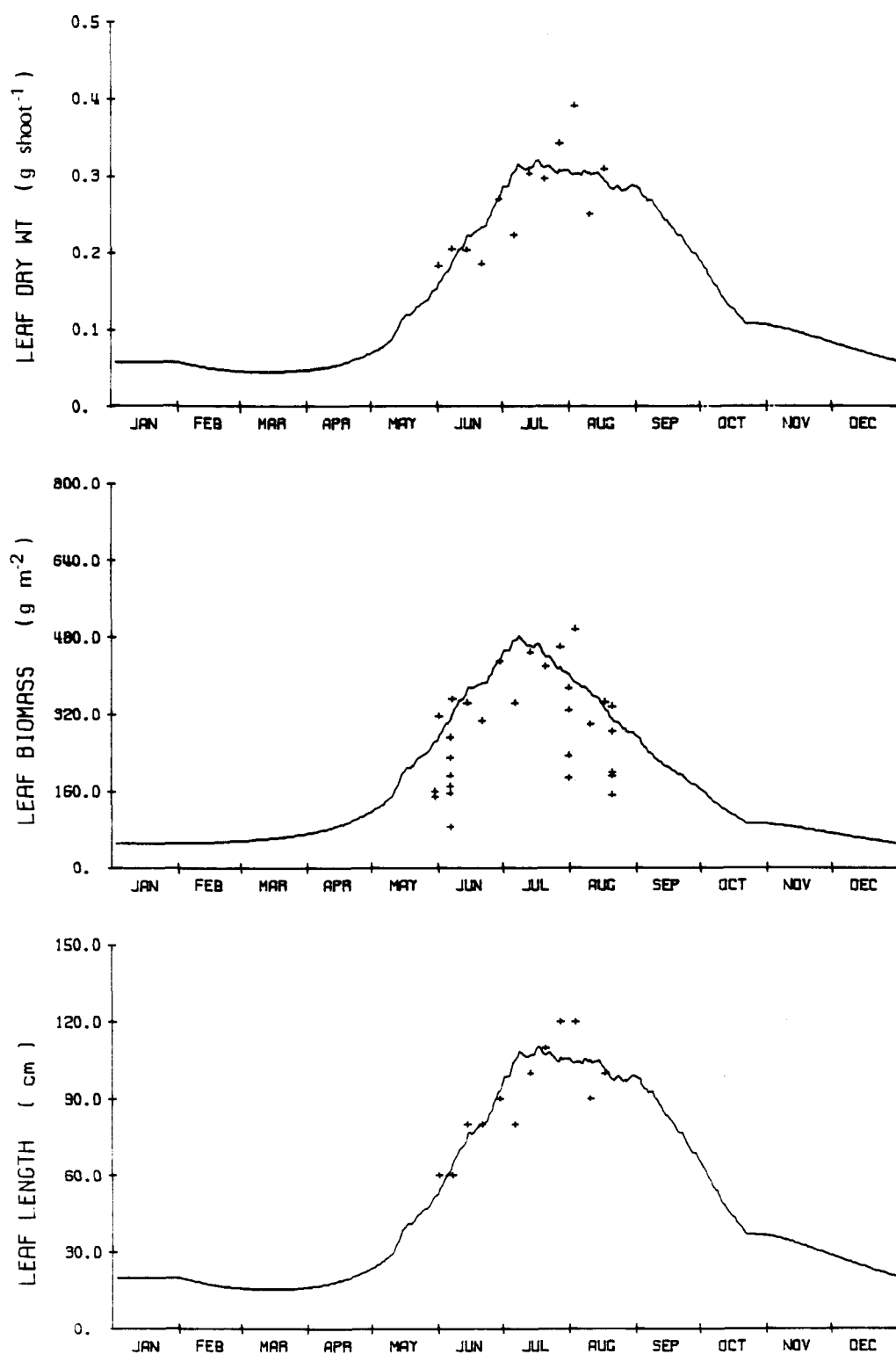


Figure 6.7. Simulated (-) and observed (+) data for eelgrass leaf dry weight per shoot, leaf dry biomass  $\text{m}^{-2}$ , and leaf length at Station 14 (Observed data from McRoy and Klug unpublished).

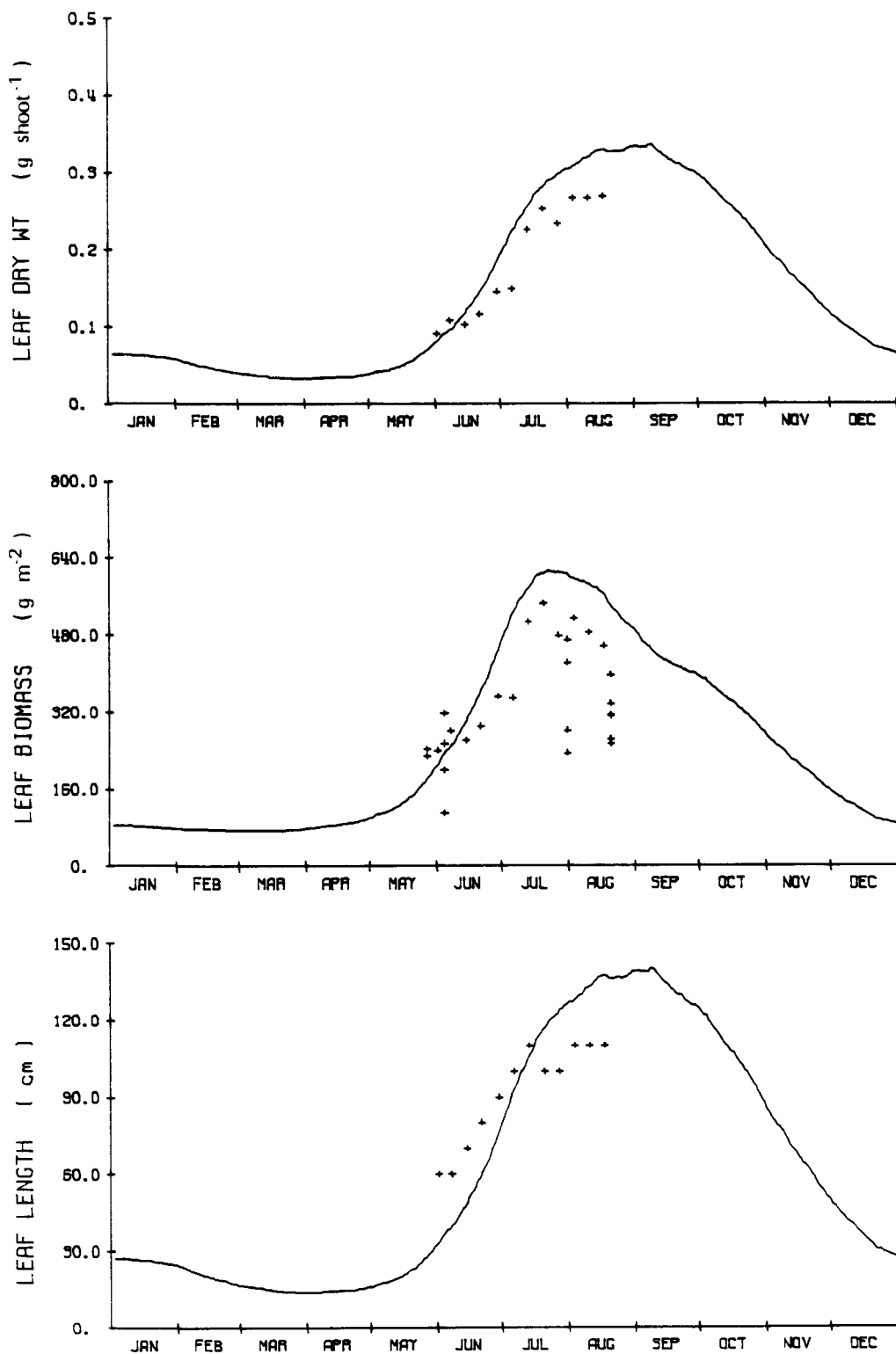


Figure 6.8. Simulated (-) and observed (+) data for eelgrass leaf dry weight per shoot, leaf dry biomass  $\text{m}^{-2}$ , and leaf length at Station 9 (Observed data from McRoy and Klug unpublished).



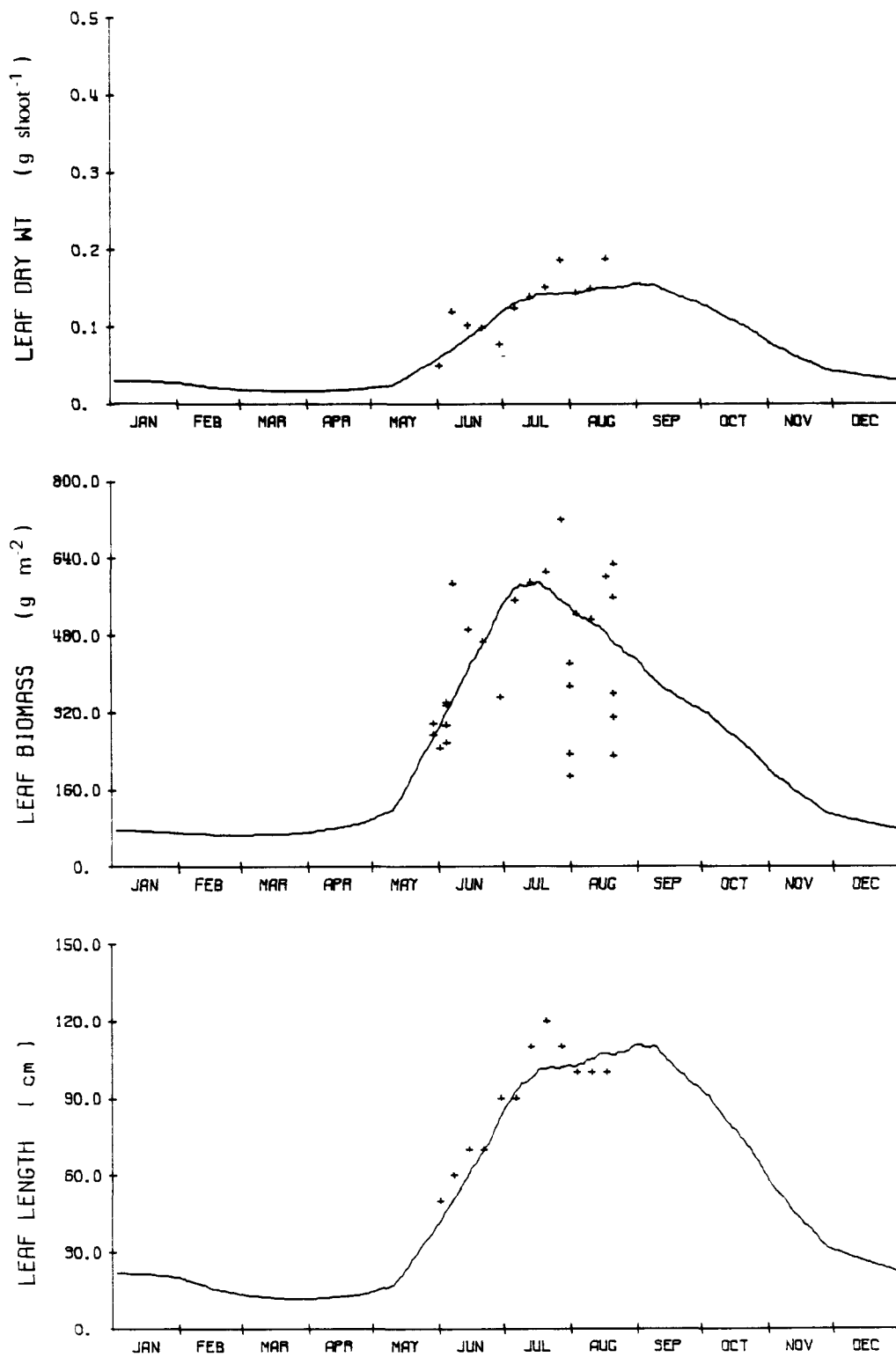


Figure 6.9. Simulated (-) and observed (+) data for eelgrass leaf dry weight per shoot, leaf dry biomass  $\text{m}^{-2}$ , and leaf length at Station 8 (Observed data from McRoy and Klug unpublished).

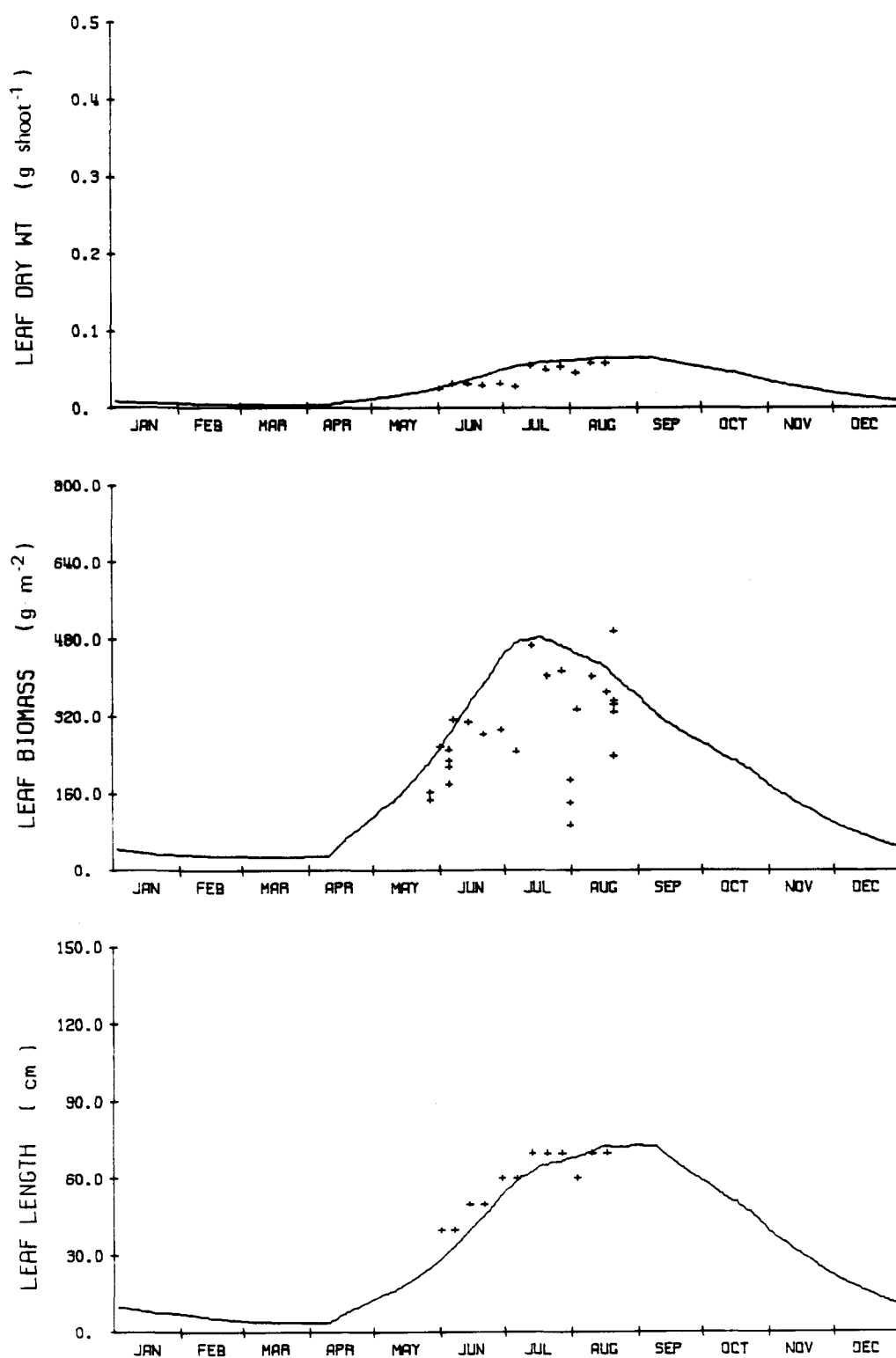


Figure 6.10. Simulated (-) and observed (+) data for eelgrass leaf dry weight per shoot, leaf dry biomass m<sup>-2</sup>, and leaf length at Station 4 (Observed data from McRoy and Klug unpublished).

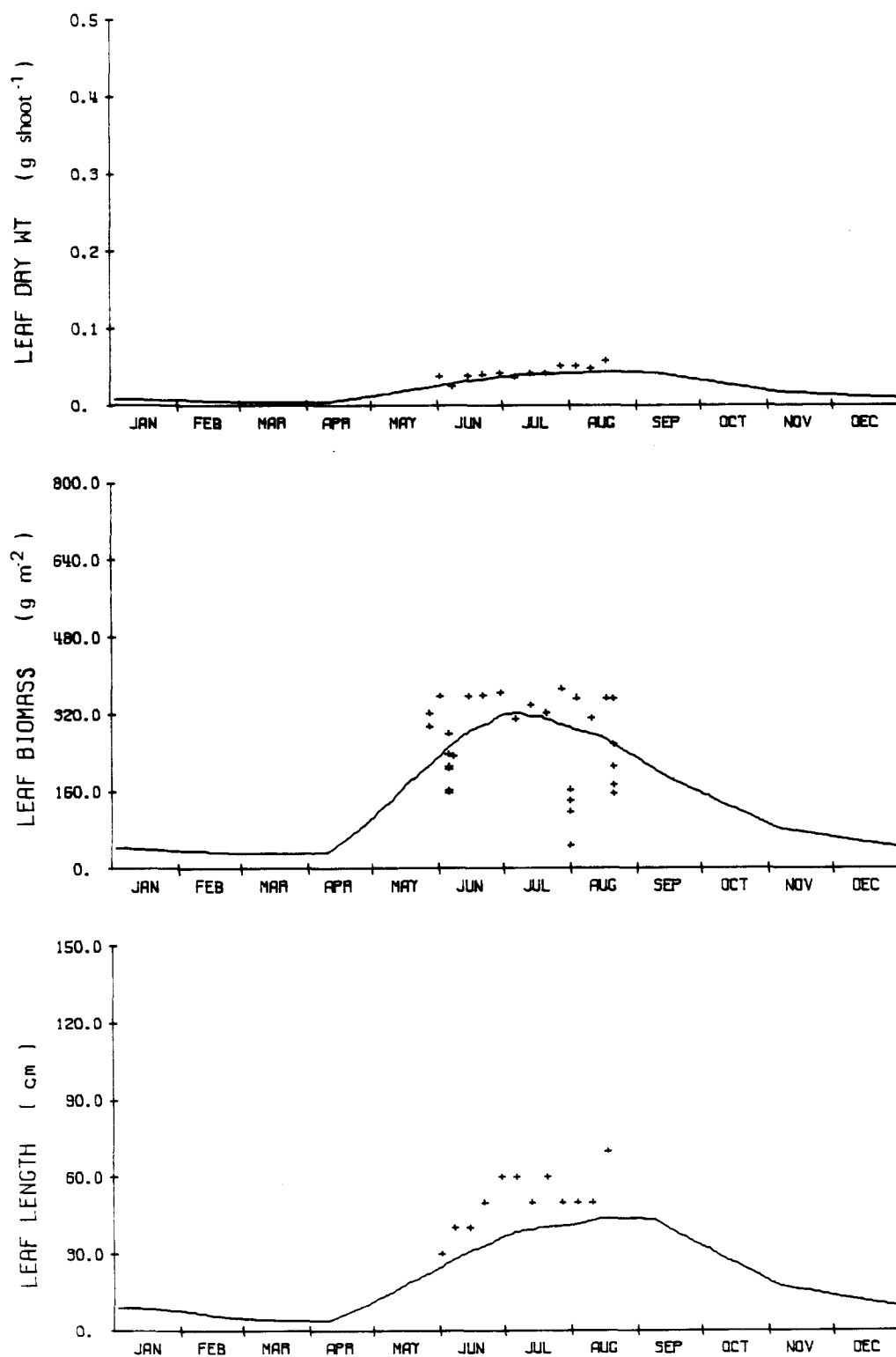


Figure 6.11. Simulated (-) and observed (+) data for eelgrass leaf dry weight per shoot, leaf dry biomass m<sup>-2</sup>, and leaf length at Station 2 (Observed data from McRoy and Klug unpublished).

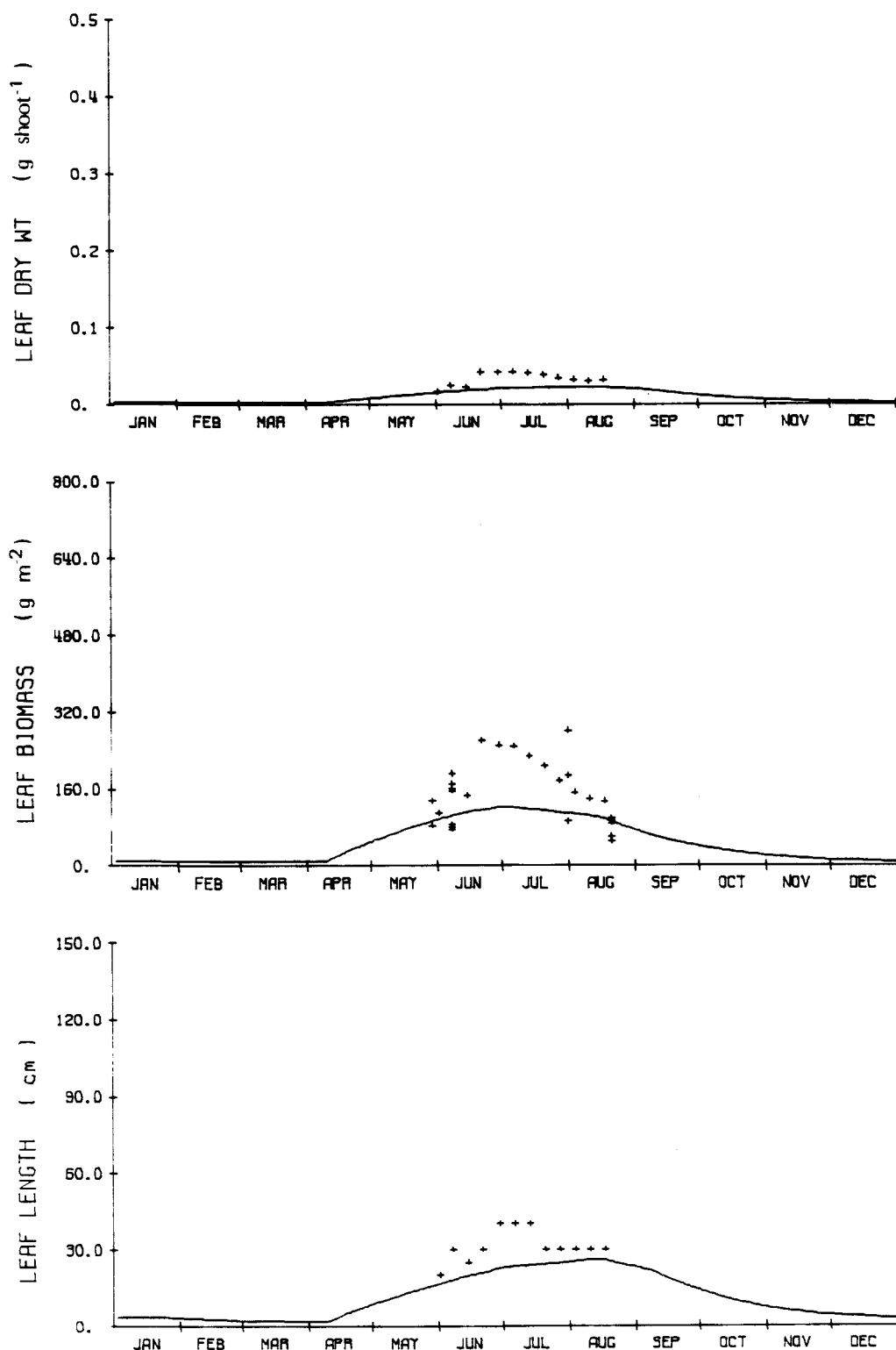


Figure 6.12. Simulated (-) and observed (+) data for eelgrass leaf dry weight per shoot, leaf dry biomass m<sup>-2</sup>, and leaf length at Station 1 (Observed data from McRoy and Klug unpublished).

data at all stations is mainly a result of the natural patchiness at the stations.

Simulation of the seasonal leaf standing stock at Station 14, the deep end of the Izembek transect, demonstrates agreement with the magnitude and seasonality of the leaf dry weight per shoot, leaf biomass  $\text{m}^{-2}$ , and leaf length data (Fig. 6.7). The model predicts maximum leaf biomass for early July at the time of maximum eelgrass growth; although biomass  $\text{m}^{-2}$  decreases after its peak, the leaf dry weight per shoot and the leaf length remain similar, with nearly constant values for two months. Similarly, the observed and simulated data for Station 9 show a peak in leaf biomass in mid-July, but both leaf length and leaf dry weight remain high until September (Fig. 6.8). The simulation of Station 9 overestimates all the standing stock measurements, especially leaf length in the fall, because leaf dry weight is overestimated and the specifications for seasonal density or environmental factors may not be appropriate. The seasonal prediction for Station 8 indicates good agreement with leaf dry weight per shoot and leaf length. However, the large variance in leaf biomass observations makes it difficult to assess this simulation (Fig. 6.9).

The leaf biomass and leaf length are essentially the same at Stations 8 and 9 in both the seasonal simulation and the observed data, but the leaf dry weight per shoot is significantly less at Station 8. The model makes it apparent that the major differences between these two stations are in shoot density and leaf width (Table 6.1). This means that with greater shoot density and smaller shoots Station 8 plants can

attain the same biomass  $\text{m}^{-2}$  as Station 9. These two stations achieve similar biomass despite differences in shoot density and leaf width because nitrogen resources (Table 2.3) influence plant morphology. That is, if the eelgrass bed with lower sediment nitrogen produces more shoots  $\text{m}^{-2}$  the plant has a greater surface area for absorbing nitrogen from both the water column and the sediments (Chapter 4).

The simulations of Stations 4, 2, and 1 show some agreement with the field data (Figs. 6.10, 6.11, and 6.12). The poor agreement between simulated and observed data in late summer for Station 1 suggests that some of the specifications in the model were not appropriate (Fig. 6.12). The overestimate of standing stock in this simulation appears to result from the high concentration of ammonium measured at this station in July (Table 2.3). The pattern of decreased standing stock across the transect from the deep stations high in sediment nitrogen to the shallow, low nitrogen areas is obvious in the field data (Table 2.1) and in the data simulated by the eelgrass model.

#### Nitrogen and Light Limitation Across Eelgrass Meadows

Eelgrass growth and biomass in the model varied substantially across the eelgrass meadow resulting in part from limited nitrogen resources in the sediments. The extent of nitrogen limitation at various stations is exemplified in plots of seasonal eelgrass growth; smooth portions of the curves depict the influence of nitrogen limitation dominating the effects of light limitation during the summer (Figs. 6.13 and 6.14). Thus, eelgrass growth alternates between periods of light

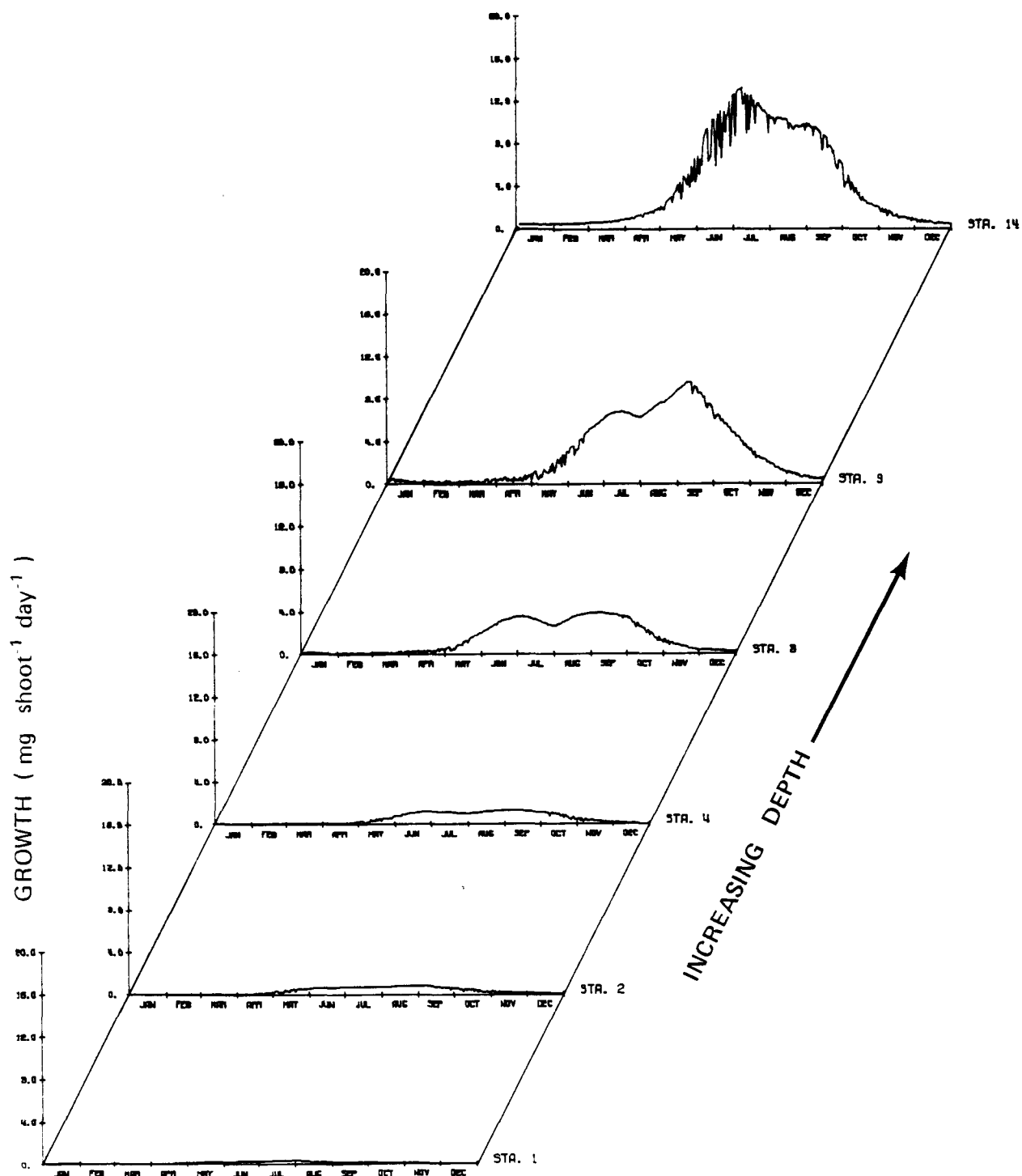


Figure 6.13. Simulation of eelgrass leaf growth (dry weight) per shoot per day for six stations along a transect.

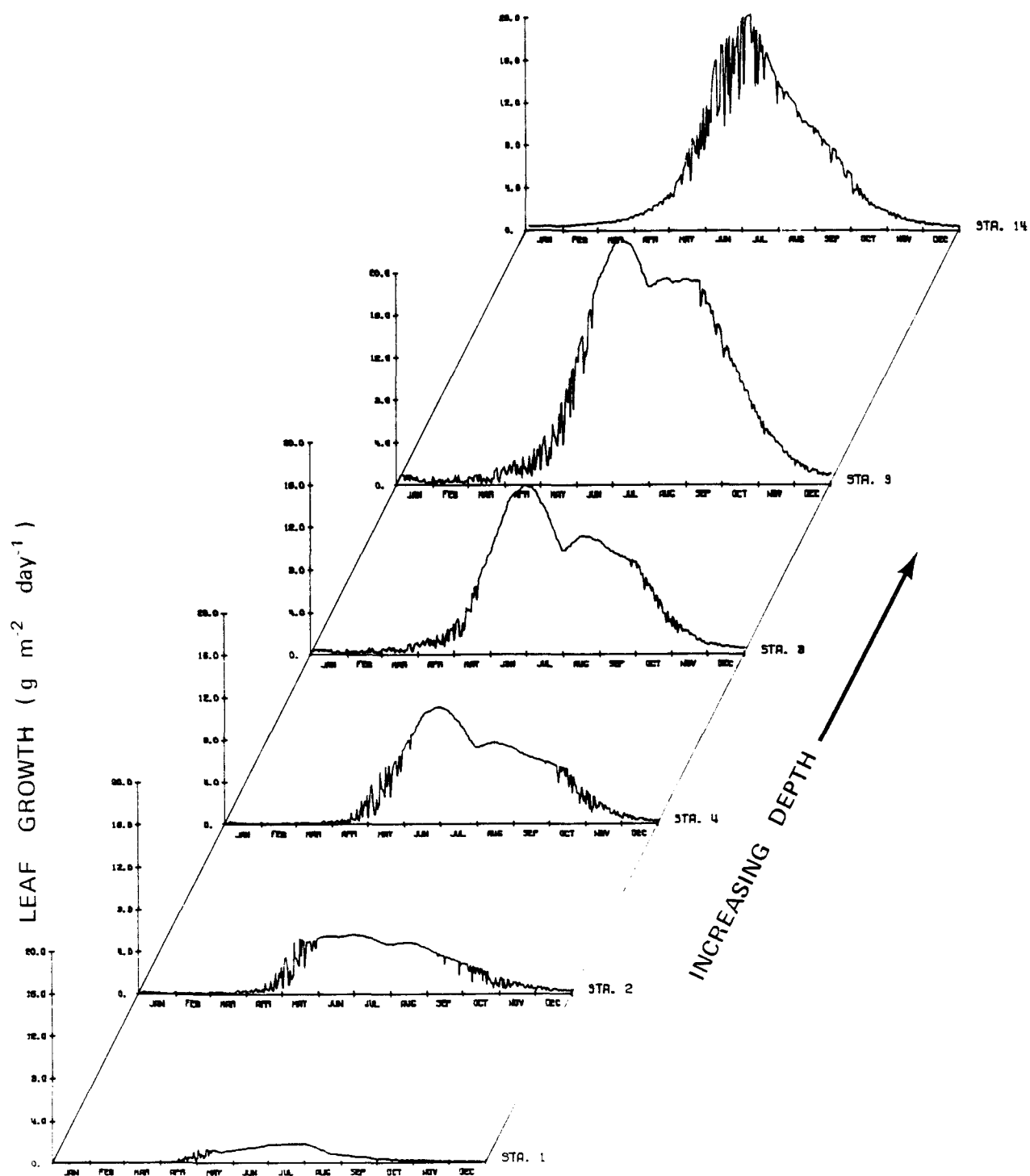


Figure 6.14. Simulation of eelgrass leaf growth (dry weight) per square meter per day for six stations along a transect.



control and periods of nitrogen control. The effect of nitrogen limitation ranges from slight reduction in light-dominated growth rates in the late summer at Station 14 to little growth throughout the summer and fall at Station 1. The nitrogen limited shoot growth at all the stations (Fig. 6.13) decreases in duration and magnitude along the transect away from shore in sediments of greater nitrogen reserves (Table 2.3). Thus, eelgrass growth per shoot across this transect illustrates the impact of nitrogen availability on shoot growth, an impact ultimately revealed in plant morphology (Chapter 3). The dip in the model-simulated growth curves around the end of July at Stations 4, 8, and 1 (Fig. 6.13) is the result of the large drop in ammonium concentrations observed in the sediments (Table 2.3).

The simulation of eelgrass leaf growth  $\text{m}^{-2}$  (Fig. 6.14) shows the spatial pattern of biomass influenced by sediment nitrogen and shoot density. The seasonal duration of nitrogen limitation is similar for leaf growth  $\text{m}^{-2}$  (smooth part of the curve, Fig. 6.14) and for growth per shoot (Fig. 6.13). Station 9 attains the largest maximum leaf growth rate per unit area of any station even though the growth rate per shoot is greater at Station 14. This disparity occurs because of the optimum combination of shoot growth and shoot density at Station 9, resulting in the greatest leaf biomass per unit area (Fig. 6.8).

The question is then: Why are the biomass and leaf growth not greater at Station 14 since there appears to be sufficient nitrogen available in the sediments (Table 2.3)? Examining the plant morphology (Table 6.1) and leaf growth rates at Station 14 (Fig. 6.14) helps to answer this question. Since the large ammonium pool in the sediments

suggests production of wide and long leaves at low density (Chapter 3), this deep eelgrass bed maximizes the leaf area in an attempt to obtain as much light energy as possible (Dennison 1979). In the model prediction, light-limited growth at Station 14 (Fig. 6.14) prevents the plants at Station 14 from exceeding the biomass or growth per unit area found at Station 9.

### Simulating Eelgrass Growth

The examination of simulated growth rates along the Izembek transect has demonstrated a large spatial and seasonal variation that is controlled by the availability of light energy (Dennison 1979) and nitrogen resources (Fig. 6.14). The simulation of eelgrass biomass is compared to the observed field data for a number of eelgrass beds (Figs. 6.7 to 6.12). Rates of change in eelgrass biomass (simulated growth rate) also require examination. The limited number of growth rate measurements for these simulated eelgrass stations provides only a small sample for estimating how well the model simulates seasonal growth rates. Observed eelgrass leaf growth during July 1977 (Iizumi 1979) near Station 8 averaged  $10.8 \text{ g m}^{-2} \text{ day}^{-1}$ , which is slightly less than the  $13.5 \text{ g m}^{-2} \text{ day}^{-1}$  calculated for the average July growth rate in the model simulation (Table 6.2). Similarly, the predicted growth rate for Station S in both June and August overestimated the rates of biomass increase measured in the field. These differences in growth rate result in part from the formulation of productivity in the model but they are largely within the natural spatial variation.

Table 6.2. Comparison of observed and simulated eelgrass growth rates for Izembek Lagoon, Alaska.

Station	Date	Leaf Growth ( $\text{g m}^{-2} \text{ day}^{-1}$ )		Reference
		Simulated	Observed	
8	July 1977	13.5	10.8 <sup>*</sup>	Iizumi, 1979
S	1-19 June 1978	5.0	4.8 <sup>**</sup>	This Study
S	12-22 August 1979	4.4	3.4 <sup>**</sup>	"

<sup>\*</sup>Growth measured as change in leaf length

<sup>\*\*</sup>Growth measured as change in biomass

### Simulating Nitrogen Enrichment

The eelgrass simulation model was used to predict the effect of fertilizing an eelgrass bed. The model experiments are similar to the field experiments of fertilizer enrichment in eelgrass beds (Orth 1977). Simulations of two eelgrass beds from the transect at Izembek Lagoon were enriched in the upper 15 cm of sediment to assess the impact on nitrogen-poor and nitrogen-rich environments. The consequences of seasonal timing of nutrient addition were examined for several months during the active growth period.

In the model, nitrogen in the form of ammonium was added to the interstitial sediment pool, increasing the average ammonium concentration by 200  $\mu\text{M}$ . This elevated concentration was maintained for one month. An enrichment simulation produced a substantial increase in eelgrass leaf growth and biomass at Station 2 during May, June, and July (Fig. 6.15). Enrichment for the month of May was least effective in stimulating leaf growth since at this season eelgrass production is primarily limited by light rather than nitrogen. The additional nitrogen did increase leaf growth significantly at the end of May and resulted in a greater biomass throughout the summer than the unenriched station (Fig. 6.11). The simulated eelgrass growth at Station 2 responded to the nitrogen enrichment during June and July by doubling the growth rate for the duration of the enrichment and by a steep increase in leaf biomass (Fig. 6.15). The increased leaf growth from the June enrichment indicated that nitrogen limitation was removed during the first two weeks, i.e., the large variation in growth rate at this time resulted from

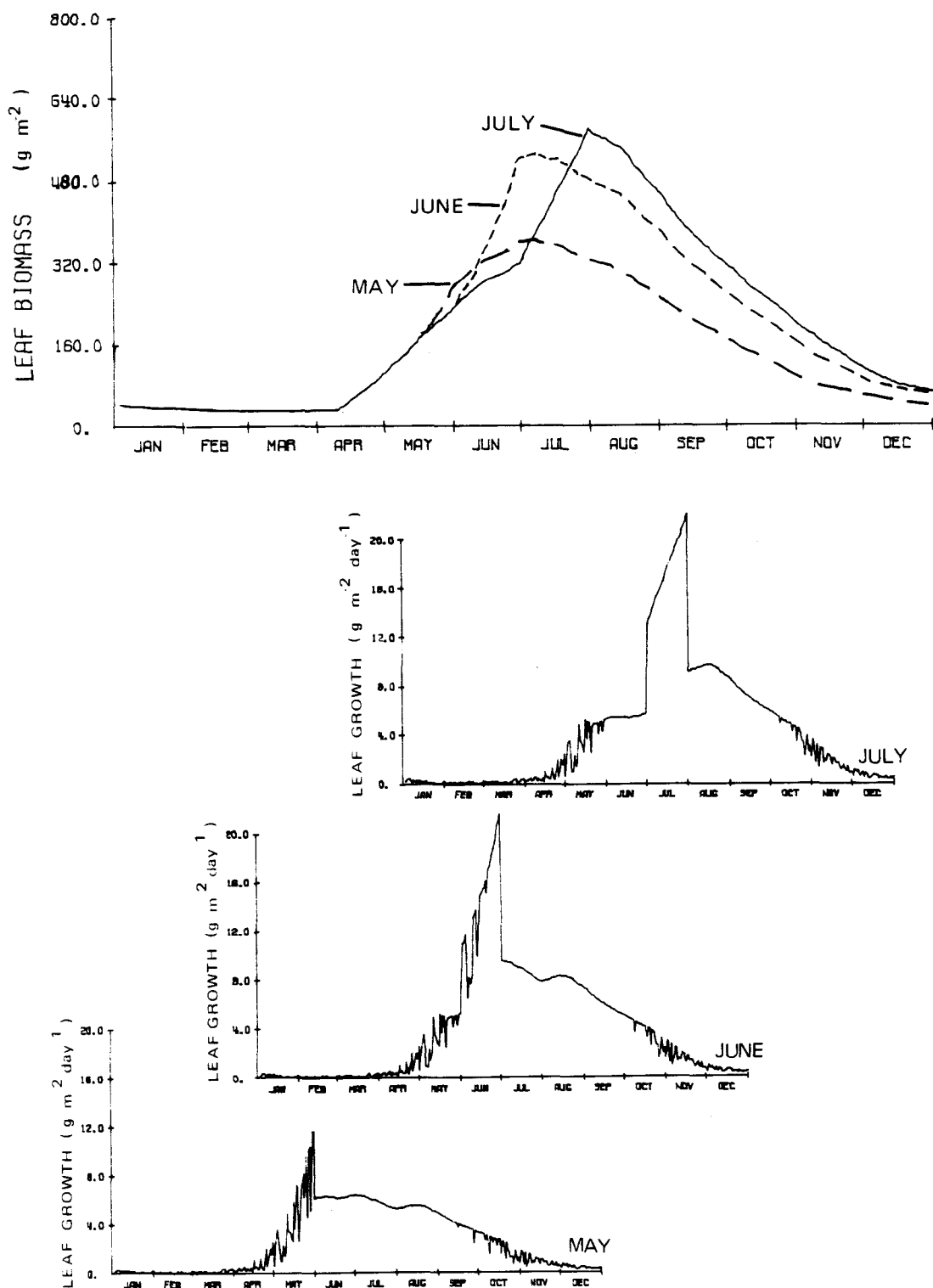


Figure 6.15. Simulated leaf biomass (upper graph) and growth (3 lower graphs) for nitrogen enrichment of nitrogen-poor Station 2: addition of 200  $\mu\text{M}$  of ammonium to the sediment nitrogen pool for each month.

light-limited growth. Near the end of the June enrichment, at high light intensities, the smoothness of the curve indicates that leaf growth is nitrogen limited even at growth rates as high as  $20 \text{ g dry wt m}^{-2} \text{ hr}^{-1}$  (Fig. 6.15). The growth rate drops at the end of the enrichment but remains higher than the rate at the unenriched station; the eelgrass leaf biomass is substantially greater after the enrichment and throughout the fall. Enrichment by the same amount of nitrogen in July increased growth but was not sufficient to completely remove nitrogen limitation (Fig. 6.15). The impact of the enrichment for the month of July was not much different than that for June, except the peak in biomass was later in the season.

As expected, the effect of increasing the sediment nitrogen concentration ( $200 \text{ } \mu\text{M}$  ammonium for a month) in an eelgrass bed growing in the nitrogen-rich sediments was less than the effect in the nitrogen-poor environment. Simulation of Station 14 with ammonium added to the sediment pool elicited no change in leaf growth or biomass for May and June; however, in July the enrichment produced a small increase in growth (Fig. 6.16). The predicted stimulation of growth is less for the nitrogen-rich eelgrass bed, Station 14, than for Station 2 with low nitrogen, since growth in the nitrogen-rich bed is primarily limited by light. The small difference in growth between the enriched and unenriched station in mid-July indicates that there are times at the unenriched station when the natural nitrogen supply could not satisfy the growth requirements (Fig. 6.7). The non-fluctuating leaf growth rates in the fall at Station 14 (Fig. 6.14) reflect a reduced nitrogen supply in the sediments resulting in periods of nitrogen limitation. The

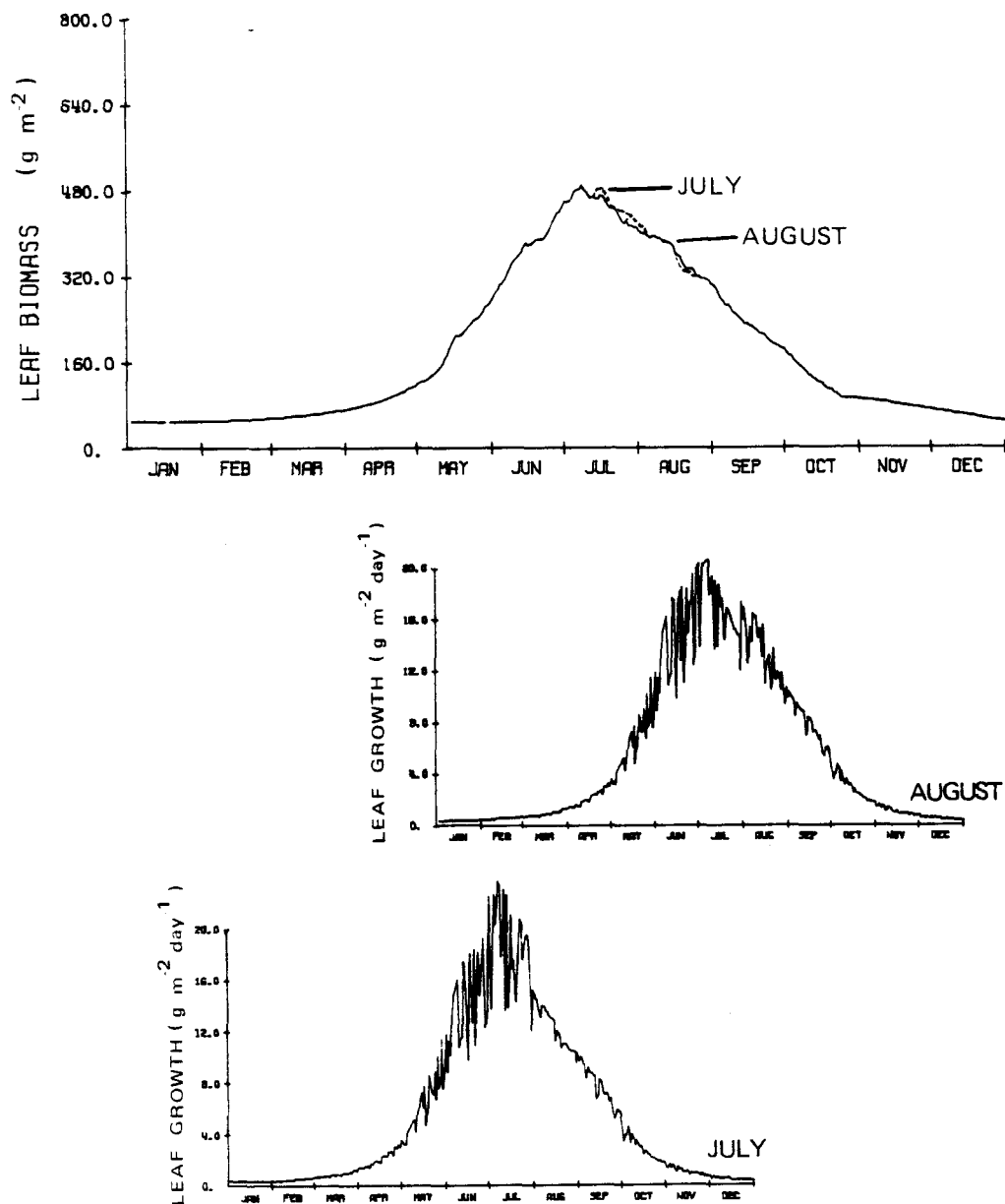


Figure 6.16. Simulated leaf biomass (upper graph) and growth (2 lower graphs) for nitrogen enrichment at nitrogen-rich Station 14: addition of 200  $\mu$ M ammonium to the sediment nitrogen pool for each month.

extent of nitrogen limitation was examined by simulating a nitrogen enrichment for the month of August (Fig. 6.16). This simulation showed higher growth rates and more evidence of light limitation (fluctuating growth curve), but the difference in biomass between the July and August enrichments was small.

The enrichments of these two stations in the model illustrate extreme conditions of the nitrogen influence on growth. Biomass in the simulations was affected only slightly in the eelgrass bed having nitrogen-rich sediments; however, in the nitrogen-poor eelgrass bed the addition of ammonium increased growth and biomass substantially. These results and those of field enrichment experiments (Orth 1977) show that the addition of nitrogen to some types of sediments stimulates growth by removing nitrogen limitation. The timing of nitrogen enrichment was important in the impact on eelgrass growth and demonstrated the alternating effects of light and nitrogen limitation.

#### Simulating Leaf Removal Perturbation

The leaf removal experiments in eelgrass beds at Izembek Lagoon enabled the estimate of eelgrass root uptake from the increase in the sediment pool after the leaves were clipped from a bed (Chapter 5). This experimental method was simulated with the model by monitoring the ammonium taken up by the plants. The results of the model experiment were used to calculate the ammonium uptake by eelgrass roots in the same manner as the field experiments.

Simulation of the plant removal experiment for Station S in July indicated an uptake rate of  $133 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$  compared to  $65 \mu\text{mole}$



$\text{N m}^{-2} \text{ hr}^{-1}$  in the field (Chapter 5). This is a relatively good agreement between predicted and observed root uptake rates considering the nature of the field experiments. Greater ammonium uptake by eelgrass roots was evident in June at Station 9, which had an experimentally determined rate of  $450 \mu\text{mole N m}^{-2} \text{ hr}^{-1}$  and a simulated rate of  $699 \mu\text{mole m}^{-2} \text{ hr}^{-1}$ . The field removal experiments probably underestimated ammonium uptake by roots by not accounting for ammonium adsorbed onto the sediments and an increased diffusion rate at higher ammonium concentrations (Chapter 5). The model, on the other hand, calculates all the ammonium taken up by the roots according to the mathematical formulation for plant uptake (Chapter 4). The eelgrass simulation model appears successful in predicting nitrogen utilization rates comparable to those measured in field perturbation experiments.

## CONCLUSIONS

The processes of model development, numerical simulation, and subsequent analysis were useful throughout this eelgrass study. Formulation of appropriate mathematical relationships utilized the seasonal abundance patterns of nitrogen availability (Chapter 2) together with the kinetics of nitrogen uptake (Chapter 4) and the analysis of plant morphology (Chapter 3) to synthesize a hypothesis of plant-nitrogen interaction. The model predicted changes in eelgrass growth and biomass in relation to nitrogen supply and simulated natural conditions.

Simulated seasonal eelgrass growth demonstrated the impact of nitrogen limitation on an eelgrass bed. The spatial distribution of

nitrogen across an eelgrass meadow allowed simulations of the extent of nitrogen utilization from the sediments and demonstrated a range of nitrogen limitation. The greatest effect occurred at the shallow end of the transect and almost no nitrogen limited growth occurred at the deeper end where the sediments were rich in nitrogen. The model showed light limitation at the deepest station throughout the year, while at other stations light-limited growth dominated only in the fall and spring.

The simulation of growth at two stations along the transect pointed out the impact of nitrogen on the extent of eelgrass development. The station with lower sediment nitrogen having a higher shoot density and smaller leaves attained approximately the same plant biomass  $m^{-2}$  as the nitrogen-rich bed through morphological variation in the plant. This supports the correlation of shoot density and leaf size to sediment nitrogen availability (Chapter 3).

Application of this model to eelgrass beds with different nitrogen resources demonstrated the ability of the simulation model to predict the effect of concentration and timing of nitrogen enrichments. The results of enriching an eelgrass bed with nitrogen either in the field or in the model provide evidence that some beds can be nitrogen limited.

The eelgrass model was used to examine the results of experimental perturbations in eelgrass beds. The simulation analysis of leaf removal experiments supports the suggestion that the field experiments underestimate eelgrass utilization of nitrogen by providing an independent calculation of ammonium uptake. However, these simulated uptake rates were similar in magnitude to the rates from the field experiments.

This modelling study consolidated the work in earlier chapters and other studies on nitrogen nutrition and growth of eelgrass. It was used to evaluate experimental and survey data relating to eelgrass physiology and distribution. The simulation of eelgrass beds with different nitrogen resources demonstrated the extent of nitrogen limitation within an eelgrass meadow. Distinguishing between nitrogen and light limitation, the model described spatial and seasonal eelgrass growth with respect to the dominant controlling factor. Simulation and manipulation of the model successfully predicted changes in eelgrass beds.

## CHAPTER 7: CONCLUSION

The intent of this research was to examine the influence of nitrogen on the productivity of eelgrass. The utilization of nitrogen by eelgrass and the dynamics of sediment nitrogen are primary processes in ecosystem nitrogen cycling. As part of a major study of nutrient processes in the eelgrass ecosystem, my research concentrated on eelgrass interaction with inorganic nitrogen resources, modelling of nitrogen utilization, and the effects of light and nitrogen on eelgrass growth.

This investigation was a response to uncertainty regarding the sources of nitrogen used by eelgrass leaves and roots, and the extent of nitrogen resources in the ecosystem. The nature of the interaction between eelgrass and the sediment nitrogen pool was proposed as a major determinant of the patterns of eelgrass standing stock. Water column nitrogen resources were also considered as part of the supply.

This research, concentrating on the eelgrass meadows in Izembek Lagoon, Alaska, included survey studies of eelgrass biomass and morphology with simultaneous measurements of sediment interstitial ammonium concentrations during the eelgrass active growing season, summer 1976-79. Experiments within specific eelgrass beds showed plant responses to manipulations of the sediment environment and, conversely, the influence of plant removal on sediment nitrogen composition. In addition, the studies of nitrogen uptake by eelgrass described a relationship between acquisition and utilization.

Some assumptions are implicit in any scientific study; among these, some aspects of ecological analysis, eelgrass biology, and modelling require examination.

- (1) The environment and associated plant community at specific locations were considered to be in a steady state condition. That is, the seasonal cycle and successional state were assumed to be unchanged from year to year.
- (2) Eelgrass, a submerged marine angiosperm, was assumed to have physiological and morphological characteristics similar to other vascular plants, both aquatic and terrestrial, making aspects of vascular plant biology available for comparison to this research.
- (3) In reference to plant nutrition, carbon, phosphorus, and nitrogen were assumed to be the major elements required for plant growth; carbon and phosphorus were assumed present in abundant supply. The nitrogen requirement was established based on carbon or phosphorus production rates available from the literature.
- (4) Utilization of an ecological model and interpretation of the simulation results required a basic assumption of the relationship between a mathematical construct and the world as observed. The mathematical relationships represented a number of individual formulations for observed interactions, and when combined in the model described relationships of greater complexity.

Eelgrass primary production is the major biological process in this ecosystem. The nitrogen available for plant growth within an eelgrass bed was hypothesized to be an important factor limiting primary production of eelgrass. Indirect evidence for nitrogen limitation is apparent from survey data showing reduced sediment nitrogen concentrations in areas of plant abundance; plant ammonium uptake from the sediment exceeds the rate of ammonium mineralization in these areas. From experimental data it is known that the rates of nitrogen uptake by both roots and leaves are not always sufficient to satisfy the requirement of eelgrass during maximum growth.

The balance between nitrogen resources and the nitrogen required for eelgrass growth was assessed using the eelgrass model. An abundance of nitrogen in simulated eelgrass beds allowed growth of large eelgrass plants; however, even using the highest sediment nitrogen concentration observed in the field, the simulated growth was limited during some times of the year. Eelgrass growth, predicted by the model for areas of low nitrogen concentration, was nitrogen limited during most of the growing season. These and other simulations over a range of sediment and water column nitrogen resources reproduced the gradient of plant biomass and morphology observed in the field studies. Thus, the model provided a method for evaluating the physiological response of the plant in relation to nitrogen available in the environment.

The question of whether eelgrass growth is nitrogen limited is difficult to answer, although the field study and the model showed a deficiency in nitrogen. Direct evidence of nitrogen limitation was provided by enrichments of eelgrass beds with nitrogen-containing

fertilizer (Orth 1977) and simulation of nitrogen enrichment in the model. The results of both studies showed that the addition of nitrogen to the eelgrass bed increased growth and produced greater plant biomass.

Growth limitation of a submerged aquatic plant can result from a number of environmental factors. Chemical factors (nutrient deficiency, toxicity, etc.) can limit growth as effectively as physical factors (light, water depth, exposure, temperature, etc.). Model simulation of eelgrass beds transecting a meadow showed seasonal and spatial controls by light and nitrogen limitation. Light manipulation experiments and leaf area distribution measurements suggested a hypothesis of light limitation on this transect (Dennison 1979). Separation of the influences of light and nitrogen as controls of eelgrass growth was presented in the eelgrass model which calculated the degree of limitation at stations on the transect. Summarizing the result of this simulation analysis in relationship to sediment nitrogen resources, the percent limitation by nitrogen and light is compared to the gradient in interstitial ammonium (Fig. 7.1). The gradient of sediment ammonium indicates that the simulated eelgrass beds are limited by nitrogen in low ammonium areas; the degree of limitation decreases in areas of greater sediment ammonium; light becomes the dominant limiting factor in the eelgrass beds at the nitrogen-rich end of the gradient. Simulation of eelgrass beds under different environmental conditions showed that the domination of one limiting factor over another changes during the year; the extent of nitrogen limitation is determined by the availability of nitrogen resources.

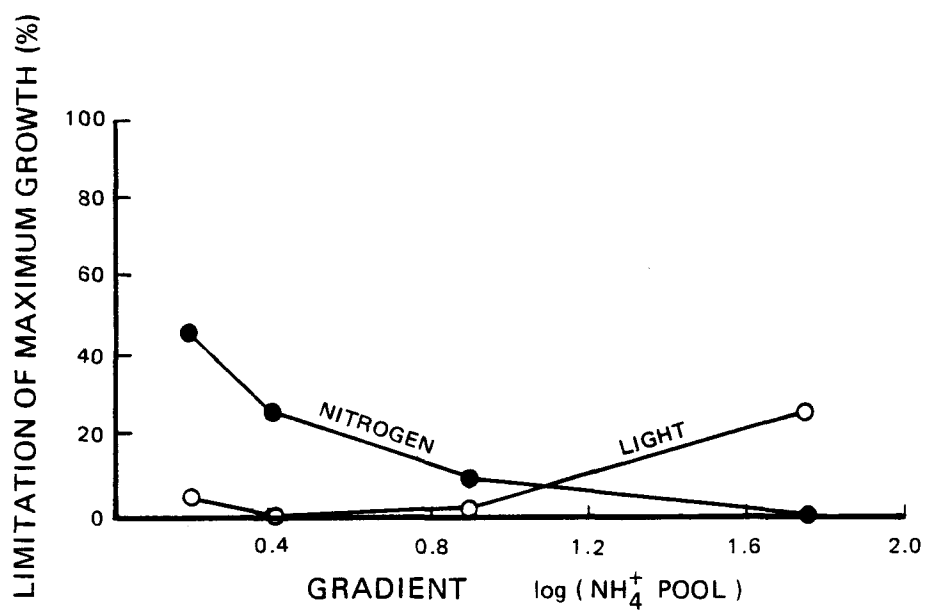


Figure 7.1. Nitrogen and light limitation of simulated eelgrass growth on July 1 for eelgrass beds on a gradient represented by the sediment ammonium pool,  $\log (\int_0^{15\text{cm}} \text{mmole N m}^{-2})$ . The greater percent limitation at each station represents the dominant limiting factor calculated by the eelgrass model (Chapter 6).



APPENDIX A: N-15 ANALYSIS METHOD AND NITROGEN  
UPTAKE DATA FOR EELGRASS

METHOD FOR THE JASCO N-15 ANALYZER

A vacuum system for preparation of  $^{15}\text{N}$  labeled eelgrass or plankton sample material was coupled to a Coleman Nitrogen Analyzer to combust samples and provide a fast and efficient technique for transferring gas samples into a discharge tube. The sample processing procedure involved combustion of the labeled material in a cupric oxide oven at  $700^{\circ}\text{C}$ , removal of oxygen gas by exposure to reduced copper, removal of carbon dioxide by freezing in a liquid nitrogen trap, and transfer of the nitrogen gas sample directly into a sample chamber. The sample gas pressure was adjusted to an optimum discharge pressure, and the gas sample was excited by radiofrequency waves producing a light emission related to the abundance of  $^{14}\text{N}$  and  $^{15}\text{N}$ . The amount of each nitrogen isotope species within the wavelength spectrum was displayed by plotting a repeating scan of the 30 peak ( $^{15}\text{N}_2$ ), 29 peak ( $^{14}\text{N} + ^{15}\text{N}$ ), and 28 peak ( $^{14}\text{N}_2$ ).

The isotope quantity was calculated from the ratios of nitrogen peak heights. The ratio  $R = \frac{\text{height } 28}{\text{height } 29}$  was calculated for small isotope quantities (when the height of the 30 peak is small), in the equation:

$$\text{apparent } ^{15}\text{N atom \%} = \frac{100}{2R + 1}.$$

The actual %  $^{15}\text{N}$  was calculated from a regression of sealed enrichments standards of known atom %  $^{15}\text{N}$  against the measured Jasco atom % values. The equation:

$$\text{actual } ^{15}\text{N atom \%} = 1.184 \times \text{apparent } ^{15}\text{N atom \%} + 0.00008$$

was used as the linear correction equation for atom %  $^{15}\text{N}$  enrichments between 0.55 atom % and 2.88 atom %. Above this range additional standards were analyzed to determine linearity.

#### Particulate Nitrogen Content

The nitrogen content of combusted samples was calculated from the pressure of gas in a constant volume of the vacuum line. The ideal gas equation provided a direct relationship between pressure and amount of gas (moles) in a constant volume at constant temperature.

The pressure of  $\text{N}_2$  gas in the vacuum line was measured in a constant volume when the gas in the system (Fig. A.1) had come to equilibrium filling the volume between the "red dot valve", the sample tube, and the valves at the other inlet/outlet locations. The pressure in torr was read directly from the gauge.

The temperature effect on the pressure of nitrogen gas in the vacuum line was minimized by maintaining a constant temperature in the area around the vacuum system. If large temperature changes could not be avoided, a correction was determined by introducing known volumes of gas at various temperatures.

To determine the particulate nitrogen content of a sample, the following pressures were recorded: the initial vacuum pressure in the system ( $P_i$ ), a set of blanks ( $P_b$ ) for the volume of gas remaining in the system when no nitrogen is combusted, and the sample gas pressure ( $P_o$ ) after combustion. The corrected pressure was calculated by the equation:

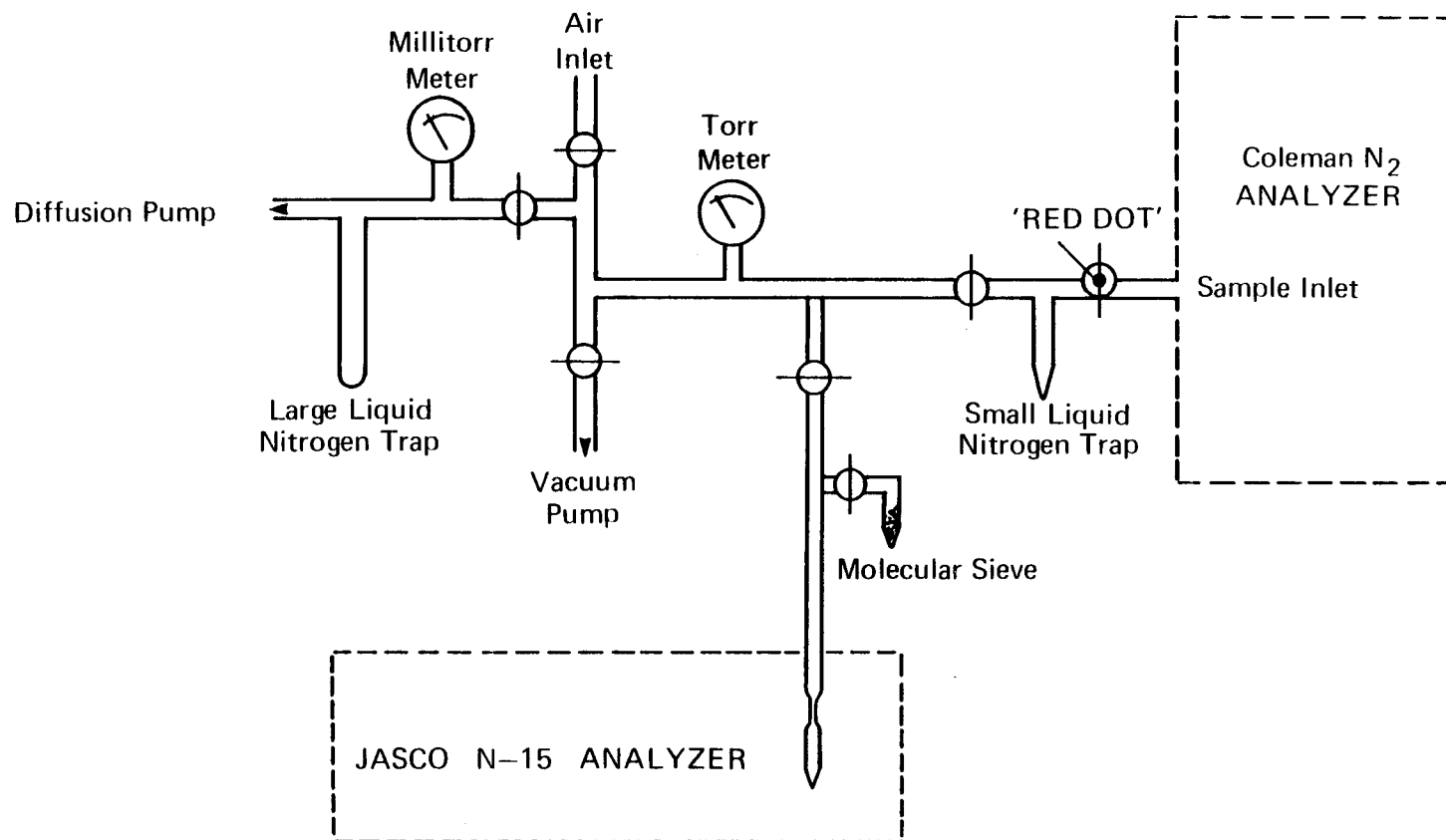


Figure A.1. Schematic diagram of the vacuum line used for preparing samples for the Jasco N-15 Analyzer.

$$P_c = P_o - (P_b + P_i).$$

The percent nitrogen in a sample was determined directly from the corrected pressure and the measured sample weight:

$$\%N = K \frac{P_c \times 100}{\text{Sample wt}}$$

with K an experimentally determined constant and a function of the volume of the system. K was calculated from combustion of weighed samples of known %N for the above system ( $K \approx 0.14$ ).

#### Pressure Effect on Discharge

The pressure of nitrogen gas in the discharge tube had a marked effect on the intensity of emission in the three wavelength bands of nitrogen. The optimum pressure described by the maximum discrepancy between the isotope peaks was determined by balancing the amount of gas sample and the volume of the discharge tube.

The relationship between the ratios of peak heights, expressed as the atom %  $^{15}\text{N}$ , and the pressure of nitrogen gas in the discharge tube was tested for a number of different atom % ratios. Two good examples demonstrated the increased pressure effect at high  $^{15}\text{N}$  atom % (Fig. A.2). The optimum pressure centered around a pressure of 2 torr, which was accepted as the sample pressure for future analyses.

Tests on the volume of the discharge tube resulted in an advantageous tube size that gave the most stable isotope ratios at 2 torr for the limited sample size.

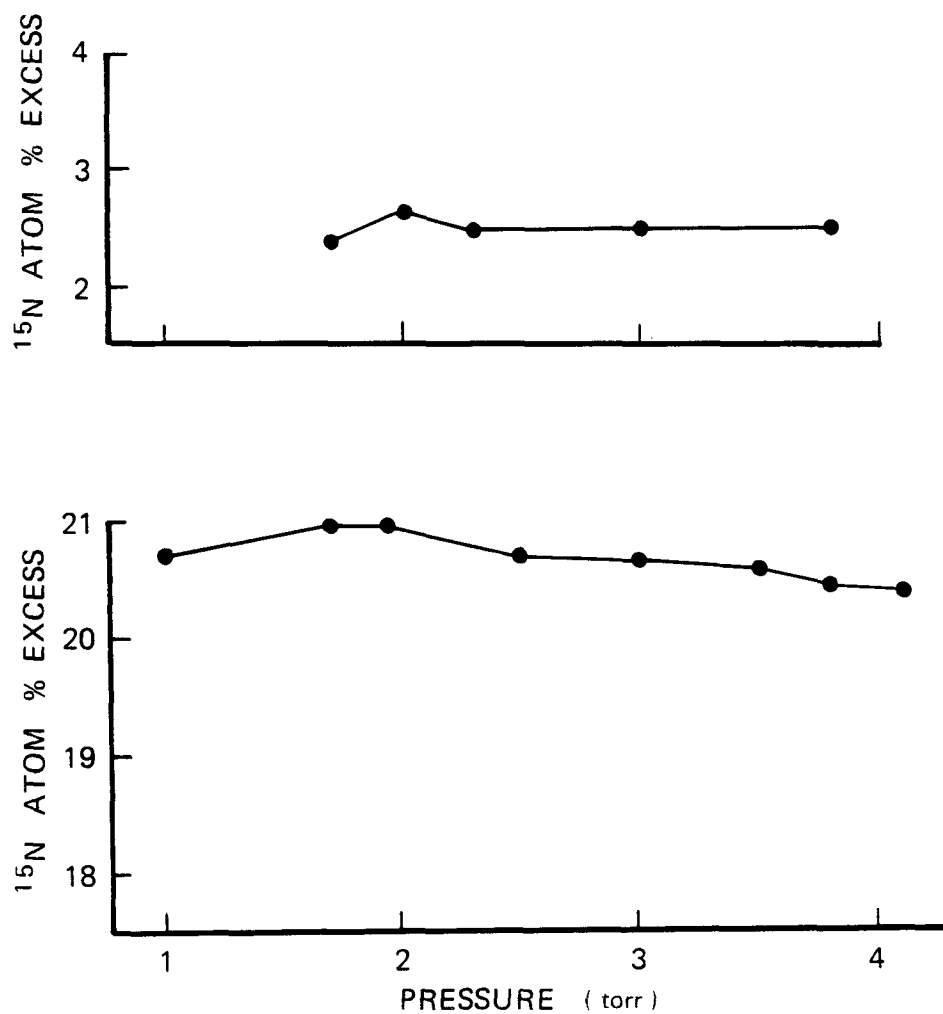


Figure A.2. Atom percent  $^{15}\text{N}$  as a function of pressure in the discharge tube of the Jasco N-15 Analyzer.

## Standardization

A set of sealed standards was made to determine a correction equation for the apparent  $^{15}\text{N}$  values produced by the Jasco N-15 Analyzer, as suggested by Lloyd-Jones *et al.* (1974). The standards were prepared by weighing out samples of unenriched eelgrass (natural abundance levels), and adding predetermined weights of  $^{15}\text{N}$  labeled ammonium chloride (99.96 atom %). The range of  $^{15}\text{N}$  enrichment, from 0.55 to 2.88 atom %, set the limits for which these standards have shown a linear response (Fig. A.3). However, the Jasco prepared standards gave a linear response to much greater atom % value. The enrichment standards were sealed in Pyrex discharge tubes as a permanent set of standards.

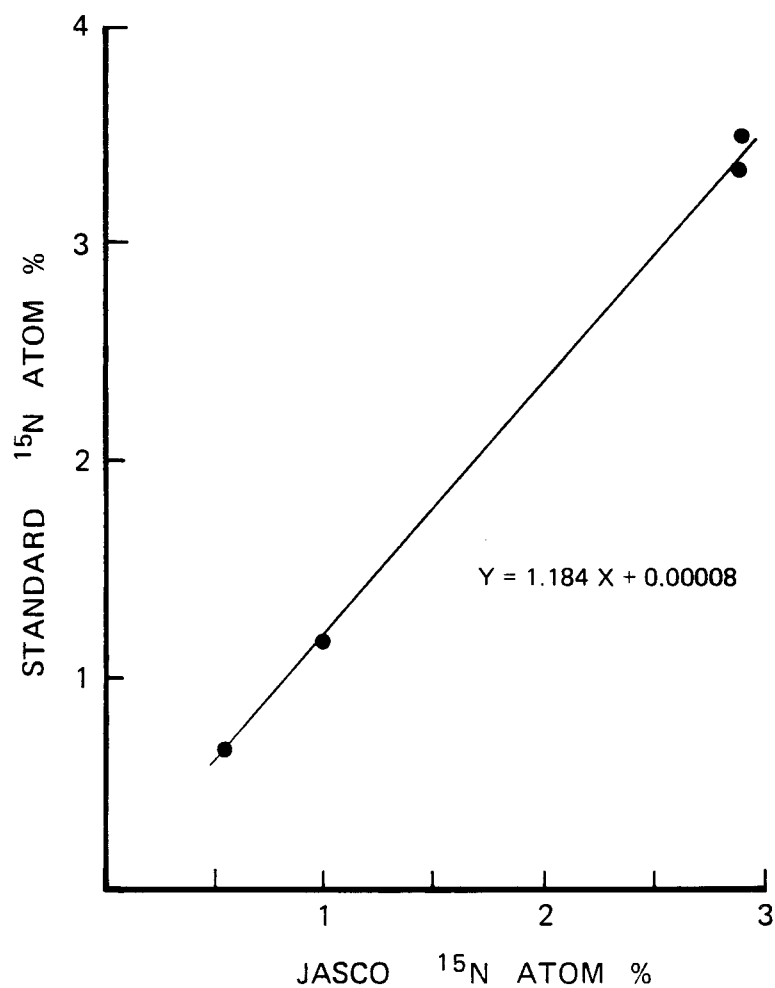


Figure A.3. Linear relationship between  $^{15}\text{N}$  atom percent in prepared standard samples and the  $^{15}\text{N}$  atom percent determined from the Jasco N-15 Analyzer.

Table A.1. Ampule experiments:  $^{15}\text{N}$ -Nitrogen uptake experiment *in situ* by eelgrass leaves in Izembek Lagoon.

Sta	Date M-D-Y	Incubation Time hr	Seawater $\text{NH}_4^+-\text{N}$ $\mu\text{M}$	Leaf			
				Added $^{15}\text{NH}_4^+-\text{N}$ $\mu\text{M}$	Uptake $\text{NH}_4^+*$	Added $^{15}\text{NO}_3^--\text{N}$ $\mu\text{M}$	Uptake $\text{NO}_3^+*$
7	7-18-77	1630-1830	3.69	7.75	7.81		
		1633-1833	"	7.87	8.36		
		1635-1735	"	7.35	10.70		
		1636-1706	"	8.20	14.01		
		1638-1648	"	7.78	32.38		
		1639-1639.5	"	9.90	168.00		
4	7-25-77	1230-1330	"	1.43	2.29		
		"	"	0.95	2.67		
		"	"	1.98	2.23		
		"	"	3.92	2.71		
7	7-27-77	1400-1500	0.24	0.95	2.65		
		"	"	1.37	3.01		
		"	"	3.92	4.57		
		"	"	7.41	7.08		
		"	"			0.82	1.35
		"	"			8.23	4.11
						18.73	9.94
15	7-30-77	1700-1800	0.88	1.01	2.82		
		"	"	1.90	2.98		
		"	"	3.81	3.88		
		"	"			0.91	1.00
		"	"			1.74	2.09
		"	"			7.55	3.66
3	8-4-77	0952-1140	0.33	3.96	2.47		
		1045-1148	"	3.57	2.61		
		1047-1117	"	3.56	5.42		
		1050-1101	"	3.38	10.11		
		1051-1054	"	3.57	10.24		
		1018-1124	"			0.69	0.62
		1020-1129	"			1.74	2.58
		1023-1130	"			7.02	4.33

\*  $\mu\text{mole N g}^{-1} \text{ hr}^{-1}$



Table A.2. Chamber experiments:  $^{15}\text{N}$ -Nitrogen uptake experiments in Izembek Lagoon. Data in parenthesis are nitrogen translocated from roots.

Sta	Date M-D-Y	Incubation Time hr	Seawater $\text{NH}_4^+-\text{N}$ $\mu\text{M}$	Leaf		Root	
				Added $^{15}\text{NH}_4^+-\text{N}$ $\mu\text{M}$	Uptake $\text{NH}_4^+*$	Added $^{15}\text{NH}_4^+-\text{N}$ $\mu\text{M}$	Uptake $\text{NH}_4^+*$
G	6-12-76	1740-1752	0.28	0.7	9.88	8.0	-
		1740-1840	"	"	2.38	"	-
		1740-2040	"	"	0.86	"	-
		1740-2140	"	"	0.69	"	-
		1740-1850	"	"	0.19	"	-
G	6-15-76	1000-1400	0.80	0.0	(0.66)	8.0	1.05
		"	"	"	(0.71)	"	1.20
		"	"	"	(0.75)	"	1.08
		"	"	"	(0.60)	40.0	1.63
		"	"	"	(0.40)	"	1.22
		"	"	"	(0.26)	"	1.37
		"	"	"	(0.40)	60.0	1.47
		"	"	"	(0.54)	"	1.73
		"	"	"	(0.47)	"	1.28
		"	"	"	(0.60)	160.0	2.41
		"	"	"	(0.46)	"	1.75
		"	"	"	(0.43)	"	2.05
G	6-16-76	1030-1430	0.53	1.3	0.97	8.0	0.77
		"	"	"	0.87	"	0.65
		"	"	"	1.32	"	0.95
		"	"	"	1.06	160.0	3.44
		"	"	"	1.03	"	1.91
		"	"	"	0.97	"	2.06
		"	"	"	1.31	240.0	2.98
		"	"	"	0.96	"	2.55
G	6-17-76	1130-1530	0.38	4.0	0.92	"	2.47
		"	"	"	2.98	8.0	0.91
		"	"	"	3.17	"	0.70
		"	"	"	2.51	60.0	1.62
		"	"	"	3.13	"	2.02
		"	"	"	2.93	160.0	2.37
		"	"	"	3.40	"	2.92
		"	"	"	3.49	240.0	3.89
G	6-18-76	1100-1500	0.58	10.0	3.52	"	3.83
		"	"	"	2.52	8.0	0.80
		"	"	"	3.40	"	0.72
		"	"	"	2.87	"	-
		"	"	"	3.21	60.0	1.06
		"	"	"	2.65	"	1.02
		"	"	"	2.74	160.0	1.16
		"	"	"	3.98	"	2.11
					3.04	240.0	1.84

\*  $\mu\text{mole N g}^{-1} \text{ hr}^{-1}$

Table A.3. Two-way analysis of variance\* with blocking tests the effect of leaf and root zone ammonium concentration on uptake by eelgrass leaves using data from Table A.2.

Source	Sum of Squares	Degree of Freedom	Mean Square	F
Mean	122.7633	1	122.7637	2323.72
Leaf Zone $\text{NH}_4^+$ -N	45.7533	3	15.2511	288.68
Root Zone $\text{NH}_4^+$ -N	0.4464	3	0.1488	2.82
Combined Error	2.6332	32	0.0823	

$$\text{Test of Leaf Zone } \text{NH}_4^+\text{-N: } F = \frac{15.2511}{0.0823} = 185.35$$

Statistically Significant  $P = 0.005$

Leaf Zone  $\text{NH}_4^+$ -N effects uptake by eelgrass leaves

$$\text{Test of Root Zone } \text{NH}_4^+\text{-N: } F = \frac{0.1488}{0.0823} = 1.808 \text{ N.S. } P = 0.10$$

Root Zone  $\text{NH}_4^+$ -N has no significant effect on uptake by eelgrass leaves.

\* BMDP2V - Analysis of Variance and Covariance with repeated measurements. Health Science Computing Facility, Univ. of California, Los Angeles 90024. November 1979.

## APPENDIX B: COMPUTER MODEL OF NITROGEN UTILIZATION BY EELGRASS

The simulation model for eelgrass in Izembek Lagoon incorporates the previous model for eelgrass production based on environmental factors (Short 1975, 1980) plus mathematical representations for nitrogen utilization by these plants (Fig. B.1). A computer model was set up for the environmental and eelgrass standing stock conditions appropriate to stations in Izembek Lagoon (Chapter 6). A functional relationship for shoot density at each station was represented by a truncated sine curve fit to the data for seasonal density (Fig. B.2).

The computer program for the eelgrass model, presented below, was written in FORTRAN for a Honeywell model 66/20B digital computer.

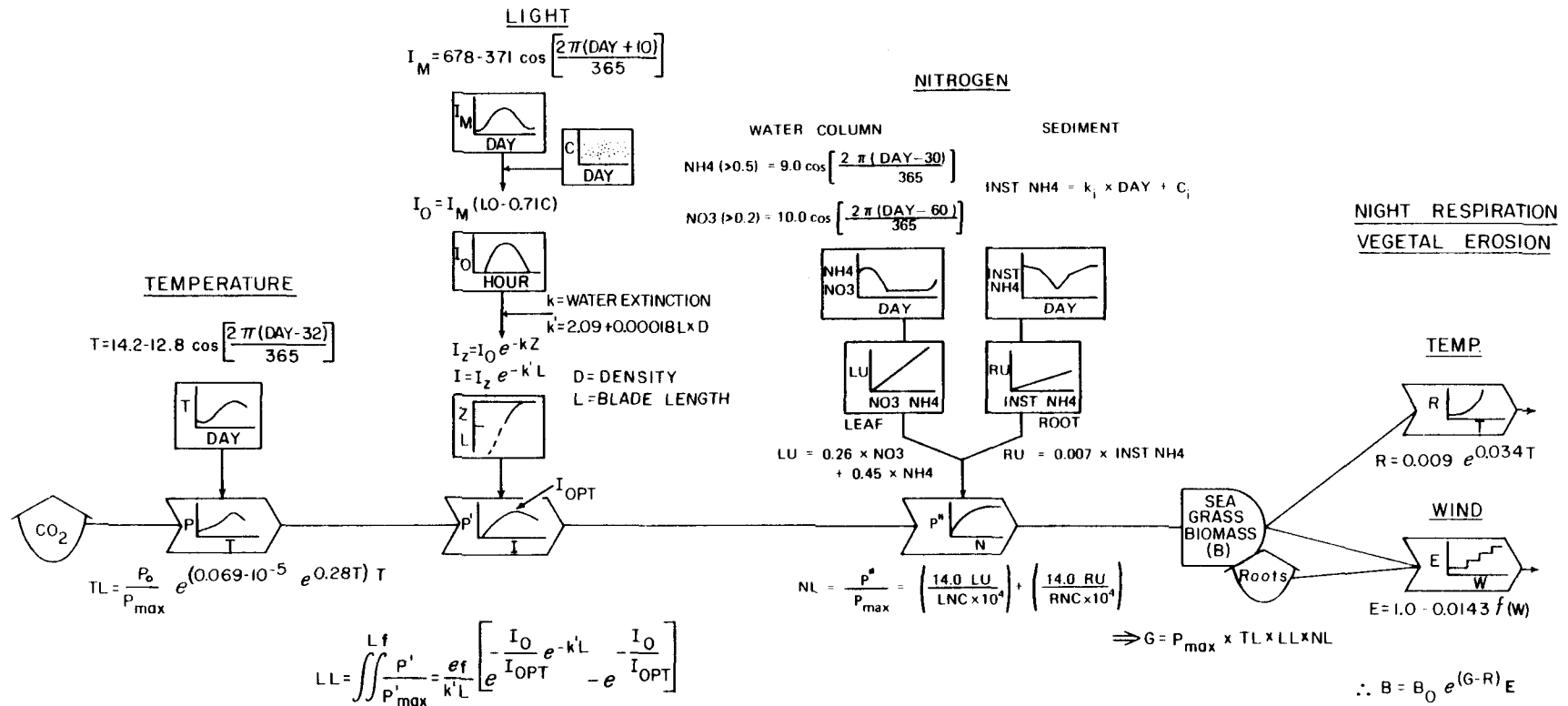


Figure B.1. Diagram of the mathematical formulation used in the eelgrass model (Adapted from Short 1975).  $P_{\max}$  - experimentally determined maximum production rate;  $P'_{\max}$ ,  $P''_{\max}$  - relative production maxima; TL - temperature limitation; LL - limitation from non-optimum light; NL - nitrogen limitation of production resulting from insufficient nitrogen; G - specific growth rate; R - night respiration; E - wind induced vegetal erosion; B - eelgrass biomass.

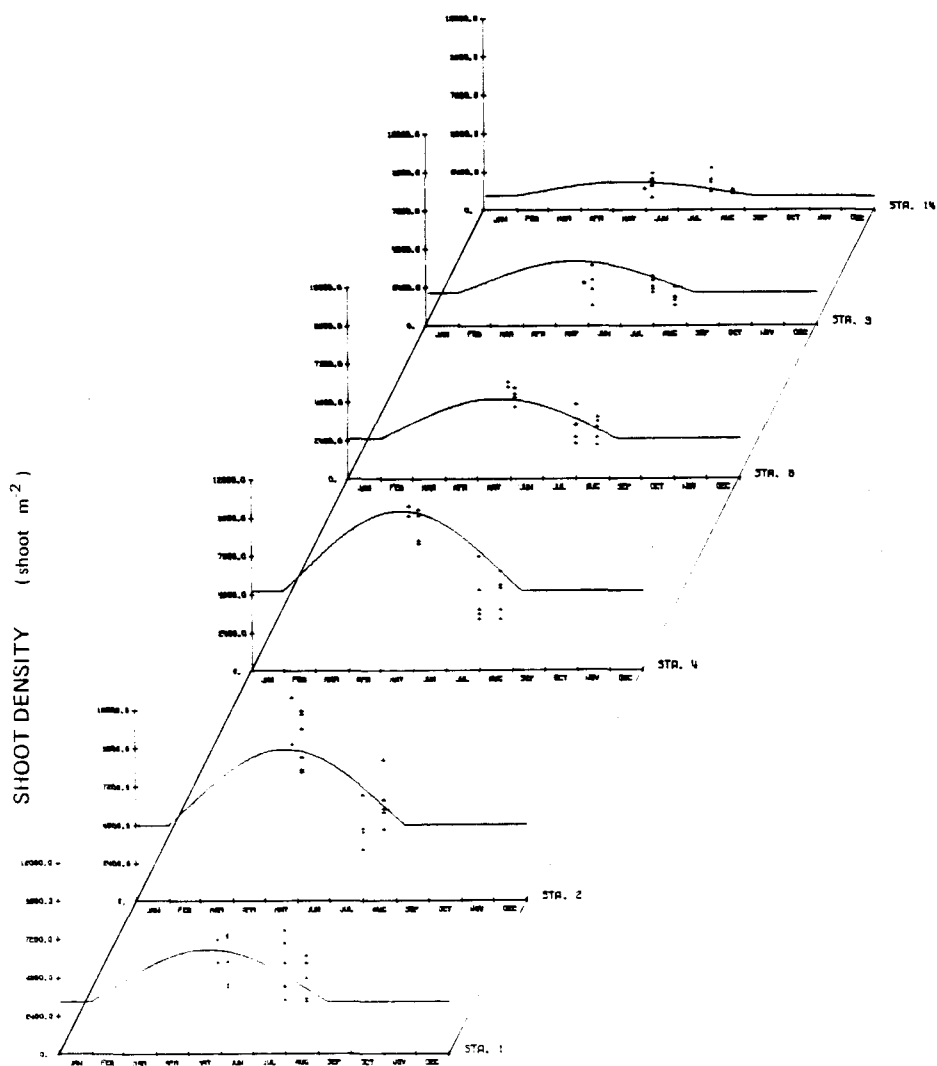


Figure B.2. Eelgrass shoot density for six stations on a transect running in Izembek Lagoon and the truncated sine curve used to represent density in the model (Observed data from McRoy and Klug unpublished).

## COMPUTER SIMULATION OF PRODUCTION IN ZOSTERA MARINA

```

C
C PLOT DATA"03", WIND DATA"04", FIELD DATA"05"
  CALL FPARAM(1,132)
C ESTABLISH INITIAL CONDITIONS FOR ELLGRASS SIMULATION
C
  IZEMBEK LAGOON, ALASKA
C STATION 14 START AUG 1
IS=14
C * DEPTH AT MEAN TIDE
DEPTH=2.0
C *ZOSTERA LENGTH IN m
ZLONG=1.49
  *ZOSTERA WIDTH IN cm
ZWISE=0.36
C *INITIALY ZOSTB IS BIOMASS FOR STARTING DAY
ZLEAF0=268.
C * INITIAL RHIZOME BIOMASS FOR STARTING DAY
ZRHIZ=719.
C * RHIZOME LENGTH
ZRL=124.8
C *EXTINCTION OF WATER IN IZEMBEK LAGOON
ECOFO=0.7
C * NO. OF LEAVES PER TURION
NLEAF=3
C *ZOST IS DENSITY IN # OF TURIONS / SQ M
ZOST=1748
  *WT. PER LENGTH IN G/M
CLENG=.29
C * ANGLE OF LATITUDE IN DEGREES
ANGLAT=55.4
  CALL BIGZ(DEPTH,ZLEAF0,ZRHIZ,ZRL,ZLONG,NLEAF,ECOFO,ANGLAT,ZOST,
& ZWISE,IS,CLENG)
  STOP
  END
  SUBROUTINE BIGZ(DEPTH,ZLEAF0,ZRHIZ,ZRL,ZLONG,NLEAF,ECOFO,ANGLAT,
& ZOST,ZWISE,IS,CLENG)
C $$ DATA FOR PLOT SUBROUTINE
  CALL PLOTST
  CHARACTER LABUTS*26(8),LABELT*12(6)
  DIMENSION X(367),Y(367,8),YO(367,8),DO(367),
& YSCLP(2,8)
  DATA LABELT/'STA. 1      ', 'STA. 2      ',
& 'STA. 4      ', 'STA. 8      ',
& 'STA. 9      ', 'STA. 14     ',
  DATA LABUTS/'LEAF DRY WT. (g/shoot) ',
& 'LEAF BIOMASS (g / sq m) ',
& 'ROOT DRY WT. (g / sq m) ',
& 'SHOOT DENSITY (# / sq m) ',
& 'LEAF LENGTH ( cm ) ',
& 'LEAF AREA INDEX ',

```

```

&          GROWTH (mg/shoot/day)
&          LEAF GROWTH (g/ sq m/ day)
DATA YSCLP/0.0,0.5,0.0,800.,0.0,1000.,0.0,12000.,0.0,150.,0.0,
& 20.,0.0,20.0,0.0,20.0/
DATA YO/2936*0.0/,DO/367*0.0/
C  $$      PLOT ROUTINE      ENDS
      DIMENSION SOLAR(32),LTLIM(32),PHOTPD(32)
      DIMENSION AMRAD(24),TEM(32),ZLEAF(8),AWRAD(53),SOLAS(700),PCOEF(8)
      REAL LTLIM,NUTLIM,KH,IOP
      INTEGER DAY, YEAR
      INTEGER MONTH(12)/31,28,31,30,31,30,31,31,30,31,30,31/
      INTEGER DATE(700)
      INTEGER ICODE(3)/'Z','T','B'/
      INTEGER LCODE(1)/'I'/
      DIMENSION BREAK(700)
      DATA ZLEAF/8*0.0/
      CALL FPARAM(1,132)
      NSIM=1
IPLT=8
      NTY=3
      IN=5
      IN=3
      JO=6
      J1=7
      PI= 3.14
      IX= 97531
      NUT=1
C  * ZDETR - DETRITUS ZOSTERA STORAGE      G-DRY /M. SQ.
      ZDETR=10.0
      ZLEAVS=ZLEAF0
      ZLONG0=ZLONG
C  MAXIMUM ZOSTERA DENSITY
      ZOSTM=ZOST
      ZOSTL =0.0
      ZLEV=ZOST
      ZNEWL=0.0
      ZDETH=0.0
      ZGRAZ=0.0
      NDLP=0
      ZPPYR=0.0
      ZWIDE=ZWIDE*.01
C  *   EXPERIMENTAL NET PRODUCTION DATA (MCROY,1974)
      Q10=2.0
      Q10P=ALOG(Q10)*0.1
      IOP=144
      TE=14.0
C  * GROWTH 1.60 MG C/G DW/HR, INST RATE 1 JULY 1973
      VMAX=1.60
C  *GROWTH PER HOUR  VMAX/0.32      DW= 32%
      VMAX=VMAX/(0.32*1000.)
C  *   RELITIVE PRODUCTION

```

```

PM=VMAX*17.4
PO= PM/EXP(Q10P*TE)
WRITE(6,45) TE,PM,PO
C  $$
  NPTS=1
  X(1)=1
  Y(1,1)=1.0
  Y(1,2)=ZLEAFO
  Y(1,3)=1.0
  Y(1,4)=1.0
  Y(1,5)=ZLONG
  Y(1,6)=1.0
  Y(1,7)=ZRL
  Y(1,8)=1.0
C  $$
  SMRAD= 0.0
  JDAY= 0
MAXM=19
MON=8
DAY=12
YEAR=1978
  ISTART= DAY+1
  IF(MON.EQ.1) MON=13
  MON0=MON
  MON=MON-1
  DT=1.0
  DO 60 I=2,MON
    II=I-1
    IF(II.EQ.MON) GO TO 60
    JDAY= MONTH(II)+ JDAY
60  CONTINUE
  MLAST=MON+MAXM
C  *****
  CALL WINDMX(BREAK)
C  *****
  DO 100 MO=MON,MLAST
    MMO=MO
    IF(MO.GT.12) MMO=MO-12
    IF(MO.GT.24) MMO=MO-24
    IF(MO.GT.12) YEAR= YEAR+ MAXM/12
    MDAYS= MONTH(MMO)
    SMRAD=0.0
    DO 200 IDAY= 1, MDAYS
      JDAY=JDAY+1
      IF(JDAY.EQ.366) JDAY=1
C *****
C   TEMPERATURE INPUT AS A COSINE CURVE: IZEMBEK DATA
C   MAX 8/16 =17C;   MIN 2/16 =0C
C   TEM(IDAY)= 10.-10.*COS(2*PI*(JDAY-31.0)/365.0)
C   TEMM=17.0
C *****

```



```

C      TOTRAD= 677.5-371.5*COS(2*PI*(JDAY+10.0)/365.0)
C      PHOTPD(IDAY)= 0.5-0.125*COS(2*PI*(JDAY+10.0)/365.0)
      CALL RADAY (JDAY,ANGLAT,DL,TOTRAD,REFLIT)
      PHOTPD(IDAY)= DL/24.
C      * PHOTOPERIOD
C      * TOTAL DAILY LIGHT RECEIVED (INSOLATION)
C      * REFLECTION OF INCOMING LIGHT AT SEA SURFACE
C *****
C      LIGHT W/ RANDOM CLOUD COVER FROM KREMER,1974
      CALL CLOUD(IX,MMO,CLDCVR)
      SOLRAD= TOTRAD*(1.0-0.071*CLDCVR)
C *****
      WD=DEPTH-ZLONG
      IF(WD.LE.0.0) WD=0.0
C      *SOLAR AND AVG RAD, ARE MEASUREMENTS OF IRRADIANCE IN LY/PHOTOPD
      SOLAR(IDAY)=SOLRAD*(1.0-REFLIT)*EXP(-ECOFO*WD)/PHOTPD(IDAY)
      SOLAS(JDAY)=SOLRAD
      SMRAD= SOLAR(IDAY)+SMRAD
C
220  CONTINUE
200  CONTINUE
      JDAI=JDAY-MONTH(MMO)
      IF(MO.LT.MON0) GO TO 110
      IF(MO.EQ.MON0) JDAI=JDAI+DAY
      AMRAD(MMO)= SMRAD/MONTH(MMO)
      IF(MO.GT.MON0) ISTART= 1
      IF(MO.EQ.MLAST) MDAYS= DAY
      DO 300 I=ISTART,MDAYS
C  DENSITY AS A FUNCTION OF TEMP WHEN I.C. ARE MAX DENSITY.
      ZOST=ZOSTM*(0.75*((COS(2*PI*(JDAI-140.)/365.))+1)/2.)+0.25)
      ZLEV=ZOSTM/2.
      IF(ZOST.LE.ZLEV) ZOST=ZLEV
      JDAI=JDAI+1
      JDAW=JDAI
      IF(JDAI.LE.30) JDAW=365+JDAI
      I30=JDAW-30
      A3ORAD=0.0
      DO 70 IM=I30,JDAW
      IMM=IM
      IF(IM.GT.365) IMM=IM-365
70  A3ORAD=A3ORAD+SOLAS(IMM)
      A3ORAD=A3ORAD/30.0
C      *CALCULATE IOP AS 50% OF THE 30 DAY HISTORY OF IRRADIANCE.
      IOP=0.50*A3ORAD
C      *EXTINCTION COEF DETERMANED FROM FEILD DATA AS FUNCTION OF DENSITY
      ECOF=2.09+0.00018*ZOST*ZLONG
      KH= ECOF* ZLONG
      SOLRAT =SOLAR(I)
      TERM1=SOLRAT /IOP
      TERM2=TERM1* EXP(-KH)
      LTLIM(I)= 2.72*PHOTPD(I)/KH*(EXP(-TERM2) -EXP(-TERM1))

```

```

PTEM=TEM(I)
C  *   ASSUME 17.0 % UPTAKE IS TRANSFERED TO RHIZOMES AND NEW LEAVES
TRRHZ=0.24
TRLVS=1.0-TRRHZ
ZPMAX=P0* EXP((0.07-0.00001*EXP(0.280*PTEM))*PTEM)
C  *   Q10 ON RESPIRATION IS 1.6 MCROY(PHD ) RANGE 1.4 TO 2.1
ZRESP=0.0107*EXP(0.047*PTEM)*PHOTPD(I)
ZNRSP=0.0107*EXP(0.047*PTEM)*(1-PHOTPD(I))
205 CONTINUE
ZPNET=ZPMAX*LTIM(I)
CALL NITRO( ZPNET,NUTLIM,JDAI)
ZPNET=ZPNET*NUTLIM
C  *   ROOT & RHIZOME GROWTH AND DEATH
ZPRHZ=TRRHZ*ZPNET
ZPNEW=EXP(ZPRHZ)-1.0
ZRK=1.
RHIN=ZPNEW*ZLEAVS*ZRK
ZNEWL=ZPNEW*ZLEAVS-RHIN
ZRLOS=0.0018
ZRHIZ=ZRHIZ+RHIN-(ZRLOS*ZRHIZ)
ZDETR=ZDETR+ZRLOS*ZRHIZ
*   LEAF GROWTH
ZPNET=ZPNET*TRLVS
ZPGROS=ZPNET+ZRESP
ZGROW=EXP(ZPGROS-ZRESP)
C  *   LEAF BREAKAGE IS 10-20% PER WEEK          WOOD, ET AL (1969)
zdeth=1.0-0.005*BREAK(JDAI)*(CLEN*10.0)
IF(ZLONG.LT.ZLONG0/4.0) ZDETH=1.0
zleavs=zleavs*zgrow*zdeth
C  *   INPUT DEAD LEAVES INTO DETRITUS
zdetr=zdetr+(1.0-zdeth)*zleavs
*   TRANSLOCATE LEAF BIOMASS
TLBIO=0.007
TRBIO=0.01
IF(JDAI.GE.230) ZRHIZ=ZRHIZ+(TRBIO*ZLEAVS)
IF(JDAI.GE.230) ZLEAVS=ZLEAVS-(TRBIO*ZLEAVS)
IF(JDAI.GT.130.AND.JDAI.LT.180) ZLEAVS=ZLEAVS+(TLBIO*ZRHIZ)
IF(JDAI.GT.130.AND.JDAI.LT.180) ZRHIZ=ZRHIZ-(TLBIO*ZRHIZ)
C  *   night time resp loss of biomass and length
zlv8am=zleavs*exp(-znrsp)+znewl
zlong= zlv8am/(cleng*zost)
zlai=(NLEAF*.66)* zwide*zlong
ZLAI=ZLAI*ZOST
ZNTLOS=ZLEAVS-ZLV8AM
ZLEAVS=ZLV8AM
ZOSTB=ZLEAVS+ZRHIZ
ZSDW=ZLEAVS/ZOST
C  *PROD  MG C / G DRY-HR
ZSTEEL=(SOLAR(I)/IOP)*EXP(1.0-SOLAR(I)/IOP)
ZPINS=(ZPMAX*TRLVS*ZSTEEL*NUTLIM)
C  * LEAF PRODUCTION ZPPHR IN mg C/g(dry)/hr

```

```

      ZPPHR=ZPINS*0.38*1000/(PHOTPD(I)*24.0)
C      *** PRODUCTION IN G /SQM / DAY
      ZPPM2=ZPNET*ZLEAVS
      ZPPSH=ZPPM2/ZOST
      ZPPYR=ZPPYR+ZPPM2
C      SET THE VARRABLES TO BE PLOTTED
C      $$      PLOT ROUTINE
      X(NPTS)=JDAI
      Y(NPTS,1)=ZSDW
      Y(NPTS,2)=ZLEAVS
      Y(NPTS,3)=ZRHIZ
      Y(NPTS,4)=ZOST
      Y(NPTS,5)=ZLONG*100.
      Y(NPTS,6)=ZLAI
      Y(NPTS,7)=ZPPSH*1000.
      Y(NPTS,8)=ZPPM2
      IF(JDAI.LE.1) NPTS=0
      NPTS=NPTS+1
      NIPS=NPTS-1
C      $$      PLOT ROUTINE      ENDS
      DATE(NPTS)=MMO*100+I
      II=I
300  CONTINUE
      MM01=MMO
      IF(MM01.GT.12) MM01=MM01-12
      WRITE(JO,1001) MM01,II ,JDAI,WD,ZLONG,TEM(II),ZDETR,ZLAI,
&      TOTRAD,CLDCVR,SOLRAD,A30RAD ,PHOTPD(II),SOLAR(II),ZLEAVS,
&      ZPMAX,LTLIM(II),NUTLIM,REFLIT,ZRHIZ,
&      ZPPHR,ZPPM2,ZGROW,ZDETH,ZGRAZ,ZOSTB
      WRITE(6,1003) ZNEWL,ZOST,ZRL,ZNRSP
      WRITE(J1,1005)MM01,II,(Y(NIPS,K),K=1,8)
1005  FORMAT(2(2X,I2),3X,8F8.2)
110  CONTINUE
100  CONTINUE
C      $$      PLOT OBSERVED DATA
      NOPTS=0
1101  FORMAT(V)
1102  FORMAT(2I3,11X,F6.0,5X,F6.2,F4.0,2F5.0)
510  READ(5,1101,END=500) NJDAY,NSTA,OSDW,OLL,OLA
      IF(NSTA.NE.IS) GO TO 510
      NOPTS=NOPTS+1
      IF(NOPTS.LE.12) GO TO 511
498  READ(3,1102,END=499) NJDAY,NSTA,ONT,OLAI,OLDW,ORDW,OTDW
      IF(NSTA.NE.IS) GO TO 498
      NOPTS=NOPTS+1
      OLL=10000.
      OSDW=10000.
      OLR=10000.0
      GO TO 512
511  OTDW=10000.0
      ORDW=10000.0

```

```

      ORL=10000.
      ONT=100000.
      OLDW=OSDW*Y(NJDAY,4)
      OLAI=OLA*Y(NJDAY,4)/10**4
512 DO(NOPTS)=NJDAY
      YO(NOPTS,1)=OSDW
      YO(NOPTS,2)=OLDW
      YO(NOPTS,3)=ORDW
      YO(NOPTS,4)=ONT
      YO(NOPTS,5)=OLL
      YO(NOPTS,6)=OLAI
      YO(NOPTS,7)=10000.0
      YO(NOPTS,8)=10000.0
      IF(NOPTS.GE.12) GO TO 498
      GO TO 510
500 CONTINUE
499 CONTINUE
      NO=NOPTS
C      $$
      CALL PTYEAR(X,Y,IPLT,DO,YO,NOPTS,LABELT,LABUTS,YSCLP,IS)
      CALL PLOT(0.,0.,999)
C      $$
CCCCCCCCCCCCCCC
999 CONTINUE
      WRITE(6,55) ZPPYR
1001 FORMAT(/'/DATE',2(1X,I2),', JDAY ',I3,',DEPTH ',F5.2,', ZLONG ',F5.2,
& ',TEMP ',F5.2,', DETR ',F10.3,', LAI ',F5.2,16X,',GRAM DRY / M**2'/
& ',TOTRAD',F10.2,', CLDCVR',F9.6,', SOLRAD',F8.1,', AMRAD',F7.1,
& ',PHOTPD',F6.2,', SOLAR',F7.1,9X,',LEAF BIOMASS',F10.4/
& ',ZPMAX ',F10.6,', LTLIM',F10.6,', NUT ',F10.6,', REFLECT ',F8.3,21X,
& ',9X,',ROOT BIOMASS',F10.4/',ZP/HR',F10.6,', ZP/M2',
& ',F10.6,',ZGROW',F10.6,', ZDETH',F9.4,', ZGRAZ',F10.6,21X,',T.',F10.4)
1002 FORMAT(' LEAF WT. ; SMLEAF',F6.1,', 2ND',F6.1,', 3RD',F6.1,', 4TH',
& ',F6.1,',5TH',F6.1,', 6TH',F6.1,', 7TH',F6.1,', 8TH',F6.1,', GM')
1003 FORMAT(' NEWL',F10.6,', # TURIONS',F6.0,', RHIZ L',F9.0,', NTRSP',
& ',F9.6)
45  FORMAT(4X,'EXP.TEMP. FROM MCROY NP  =',F5.2,', C',
& ',/4X,',MAX PRODUCTION @ EXP TEMP =',F8.6,', G/G/DAY',
& ',/4X,',MAX PRODUCTION @ 0 C =',F8.6,',G/G/DAY')
55  FORMAT(/' TOTAL BIOMASS PRODUCED PER YEAR =',F12.2)
99  FORMAT(1H1)
      RETURN
      END
      SUBROUTINE WINDMX(BREAK)
      INTEGER WSPD
      DIMENSION ITEM(365),IDIRC(365),ISPED(365)
      DIMENSION BREAK(365)
      IN=5
      IN=4
1000 FORMAT(10(I2,1X,2I2,1X))
      READ(IN,1000)(ITEM(J),ISPED(J),IDIRC(J),J=1,365)

```

```

DO 10 I=1,365
IF(ISPED(I).EQ.99) ISPED(I)=0
WSPD=ISPED(I)
BREAK(I)=1.0
IF(WSPD.GT.14) BREAK(I)=2.0
IF(WSPD.GT.21) BREAK(I)=3.0
10 CONTINUE
RETURN
END
SUBROUTINE CLOUD(IX,MO,CLD)
C CLOUD COVER SUBROUTINE TO GENERATE RAMDOM CC DATA WITHIN
C AN OBSERVED DISTRIBUTION, GLOBAL ATLAS FO RELITIVE CC 1967-60
C FEB 27 1978
C
  DIMENSION CFEW(12),CSOME(12),CMANY(12)
  DATA CFEW/20.,20.,10.,10.,30.,30.,30.,20.,10.,10.,10.,20./
& CSOME/40.,50.,40.,40.,30.,20.,20.,20.,30.,40.,40.,40./
& CMANY/40.,30.,50.,50.,40.,50.,50.,60.,60.,50.,50.,40./
  CALL RANDU(IX,IY,YFL)
  YFL=6.666667*ABS(YFL)
  AMANY=CFEW(MO)+CSOME(MO)+CMANY(MO)
  ASOME=CFEW(MO)+CSOME(MO)
  AFEW=CFEW(MO)
  IF(YFL.LT.ASOME) GO TO 1
  YMAX=AMANY
  YMIN=ASOME
  XMIN=6.6667
  GO TO 5
1 IF(YFL.LT.AFEW) GO TO 2
  YMAX=ASOME
  YMIN=AFEW
  XMIN=3.3333
  GO TO 5
2 CONTINUE
C YFL. LT .AFEW
  YMAX=AFEW
  YMIN=0.0
  XMIN=0.0
5 CLD=XMIN+3.0*(YFL-YMIN)/(YMAX-YMIN)
  IX=IY
  RETURN
END
SUBROUTINE RANDU(IX,IY,YFL)
C SUBROUTINE RANDU FROM SSP IBM
  IY=IX*65539
  IF(IY)5,6,6
5 IY=IY+2147483647+1
6 YFL=IY
  YFL=YFL*0.4656613E-9
  RETURN
END

```

```

SUBROUTINE RADAY(ND,ALAT,DL,QEXT,REFL)
C SUBROUTINE RADAY TO GIVE DAY LENGTH AND RADIATION LEVELS
C FROM 'GRAZING SYSTEMS NEWSLETTER' NO. 6 2ND REPLACEMENT PG.
  FN=ND
C ND = DAY OF YEAR
  THETA=0.0172142*(FN-172.)
  SDCLN=0.00678+0.39762*COS(THETA)+0.00613*SIN(THETA)
& -0.00661*COS(2.*THETA)-0.00159*SIN(2.*THETA)
  DCLN=ARSIN(SDCLN)
C DCLN= DECLINATION OF THE SUN
  RLAT=ALAT*0.0174533
C ALAT= LATITUDE OF SITE IN DEGREES (NEGATIVE FOR SOUTHERN HEMISPHERE)
  DNLAT=-TAN(RLAT)*TAN(DCLN)
  HRANG=ARCOS(DNLAT)
C HRANG= HOUR ANGLE
  DL=7.639437*HRANG
C DL= DAYLENGTH IN HOURS (PHOTOPERIOD)
  QEXT=916.73*(HRANG*SIN(RLAT)*SDCLN+SIN(HRANG)*COS(RLAT)
& *COS(DCLN))
C QEXT= RADIATION OUTSIDE EARTHS ATMOSPHERE (CAL/CM2/DAY)
C QEXT DOES NOT TAKE INTO ACCOUNT THE VARIATION IN SUN EARTH DISTANCE.
C VALUES ON JAN. 1 3.5% TOO HIGH. VALUES ON JULY 4 3.5% TOO LOW.
C ATMOSPHERIC ABSORPTION OF SOLAR RADATION
C ~0.70 TRANSMISSION COEF. FOR CLEAR SKY RAD.OVER THE OCEAN
C FROM REED,R. 1977. ON EST. CLEAR SKY INSOL. J.P.O.
  QEXT=QEXT*0.7
C
C ZENITH = SUN'S ZENITH DISTANCE
C FROM SIMITHSONIAN METEOR. TABLE (1966) P 417
  COSZ=SIN(RLAT)*SIN(DCLN)+COS(RLAT)*COS(DCLN)*SIN(HRANG)
  ZENITH= ARCOS(COSZ)
C
C REFLECTIVITY OF SEAWATER
C ( S.M.T. P155
C XN = INDEX OF REFRACTION SW OF 35 PPT N= 1.3398
  XN= 1.3398
C AOR = ANGLE OF REFRACTION
  AOR=ARSIN(SIN(ZENITH)/XN)
C REFL = REFECTIVITY
  REFL=(((SIN(ZENITH-AOR))**2)/((SIN(ZENITH+AOR))**2))+
& (((TAN(ZENITH-AOR))**2)/((TAN(ZENITH+AOR))**2))
  REFL=REFL*0.5
  RETURN
  END
  FUNCTION TAN(X)
  TAN= SIN(X)/COS(X)
  RETURN
  END
C
SUBROUTINE NITRO(ZPNET,NUTLIM,JDAY)
C

```

## CALCULATE THE EFFECT OF NITROGEN LIMITATION

```

C
  REAL NUTLIM
C  INITIAL CONC.
  WCNH4=9.0*COS(2.*3.14*(JDAY-60.)/365.)
  IF(WCNH4.LE.1.5) WCNH4=1.5
  WCNO3=10.0*COS(2.*3.14*(JDAY-30.)/365.)
  IF(WCNO3.LE.0.2) WCNO3=0.2
  SNH4=870.8
  IF(JDAY.GT.169) SNH4=-8.61*JDAY+2325.
  IF(JDAY.GT.212) SNH4=-1.73*JDAY+867.
  IF(JDAY.GT.233) SNH4=3.08*JDAY-254.1
C  EELGRASS N CONTENT
  ZLNC=0.024
  ZRNC=0.017
C  EELGRASS UPTAKE
C  REGRESSION FOR N UPTAKT AT CONC> 0.4UM
  ZLUNH4=0.45*WCNH4
  ZLUNO3=0.26*WCNO3
C  EELGRASS ROOT UPTAKE
  ZRUNH4=0.0074*SNH4*.9
C  PLANT UPTAKE FOR 24 HR
  ZNP=((ZLUNH4+ZLUNO3)*14.0 /((ZLNC*10**6)
&      +(ZRUNH4* 14.0)/(ZRNC* 10**6))
  ZNP=ZNP*24.
C  NITROGEN REQUIREMENT FOR THE PHOTOPERIOD
  ZNREQ=ZPNET
C  N LIMITATION
  IF(ZNP.GE.ZNREQ) GO TO 10
  NUTLIM=ZNP/ZNREQ
  GO TO 20
10  NUTLIM=1.0
20  CONTINUE
  RETURN;END

```

## APPENDIX C: A RELATIONSHIP BETWEEN INTERSTITIAL AMMONIUM CONCENTRATIONS AND THE CONCENTRATION AT THE ROOT SURFACE

General depletion of interstitial ammonium concentrations resulting from uptake by eelgrass roots was demonstrated in Chapters 2 and 5; however, the specific gradients of concentration in the root zone were not examined. To determine the extent of concentration depletion at the root surface models of nutrient reduction by terrestrial plant roots (Olsen and Kemper 1968; Nye and Tinker 1977) were examined. A model (Nye *et al.* 1975) calculating the nutrient concentration at the root surface from the average nutrient concentration throughout the root zone was selected for this analysis. The radial flow of nutrients to the roots is assumed to be the limiting step in uptake, implying that uptake per root length is a more appropriate consideration than uptake per surface area. Additional assumptions are that the soil cylinders which the roots exploit do not overlap, and that the effect of mass flow through the soil is not important. Generally these are acceptable although for many eelgrass beds the assumption of non-overlapping zones around the roots is questionable.

The expression for nutrient concentration at the root surface,  $C_{la}$ , is a function of the average concentration in the sediments,  $\bar{C}_l$ , and the characteristics of the plant, the sediments, and the ion being considered (Nye *et al.* 1975).

$$C_{la} = \bar{C}_l \left( 1 + \frac{\alpha \bar{a}}{Db} \ln \frac{x}{1.65a} \right)^{-1}$$

where  $D$  = diffusion coefficient of the solute,  $\text{cm}^2 \text{ s}^{-1}$   
 $b$  = buffer power of the soil  
 $\alpha$  = root absorbing power,  $\text{cm s}^{-1}$   
 $\bar{a}$  = average root radius,  $\text{cm}$



$$x = (\pi L_v)^{-\frac{1}{2}} = \text{average radius of the soil cylinder exploited, cm}$$

$$L_v = \text{root density (length per unit volume of soil), cm}^2$$

The concentration difference between the average interstitial ammonium concentration and the ammonium concentration in contact with the root surface was examined for an eelgrass bed to determine the magnitude of this gradient. A diffusion coefficient for ammonium, neglecting adsorption,  $D = 4.0 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$ , was chosen as a representative value for marine muds (Krom and Berner 1980). The buffer power of the sediment related to the equilibrium ratio of exchangeable to interstitial ammonium ( $b \approx 2$ ; Blackburn 1979b). The absorbing power of eelgrass roots is estimated by comparison to data for ammonium uptake (Nye and Tinker 1977) by rice roots ( $\alpha = 0.75 \times 10^{-4} \text{ cm s}^{-1}$ ) and maize roots ( $\alpha = 2 \times 10^{-4} \text{ cm s}^{-1}$ ) as  $\alpha = 1 \times 10^{-4} \text{ cm s}^{-1}$ . An average root radius and root density are calculated from measurements of eelgrass root size (Smith *et al.* 1979):  $\bar{a} = 0.017 \text{ cm}$  and  $L_v = 27.6 \text{ cm}^{-2}$ .

The concentration of ammonium at the eelgrass root surface is calculated from the above equation assuming an average interstitial ammonium concentration  $\bar{C}_\ell = 100 \text{ } \mu\text{M}$ . The resulting ammonium concentration at the root surface,  $C_{\ell a} = 78 \text{ } \mu\text{M}$ , indicates a 22% reduction in ammonium concentration.

The estimate indicates that the reduction in ammonium in the sediment cylinder around the roots could decrease the ammonium uptake rate by eelgrass roots. However, the variations in the diffusion coefficient and sediment buffering power for different sediment types are significant. Observed differences in root size and density as well as the

extent of root hair development in eelgrass plants from various environments suggests that examination of all these parameters in specific eelgrass beds is necessary to determine the real extent of root zone depletion.

# APPENDIX D: DATA FROM SEDIMENT CORE SAMPLES

## COLLECTED AT IZEMBEK LAGOON, ALASKA

Table D.1. Ammonium concentrations and sediment characteristics.

Date M-D-Y	Station	Sediment Depth cm	Sediment Porosity ml cm <sup>-3</sup>	Inst NH <sub>4</sub> <sup>+</sup> -N μM	Sediment Density g cm <sup>-3</sup>	Exc NH <sub>4</sub> <sup>+</sup> -N μM	Notes
6-24-76	S	0-5	9.92	48.3			
		5-10	0.77	216.7			
		10-15	0.75	249.5			
	S	0-5	0.91	40.0			
		5-10	0.83	289.0			
		10-15	0.73	286.7			
	S	0-5	0.98	16.4			
		5-10	0.81	241.5			
		10-15	0.70	220.5			
	S	0-5	0.96	26.6			
		5-10	0.81	200.1			
		10-15	0.71	247.4			
6-30-76	S	0-5		39.1			
		5-10		36.4			
		10-15		97.3			
		15-20		123.9			
		20-25		111.6			
	S	0-5		59.4			
		5-10		31.3			
		10-15		74.8			
		15-19		117.8			
		0-5		60.9			
	S	5-10		45.6			
		10-15		142.3			
		0-5		57.9			
		5-10		42.5			
		10-15		117.8			
	S	15-20		113.7			
		20-25		99.3			
		0-5		68.5			
		5-10		66.0			
		10-15		121.9			
	S	15-20		144.4			
		20-25		135.2			
		0-5		29.2			
		5-10		34.3			
		10-15		97.3			
		15-20		125.9			
		20-25		113.7			

Date M-D-Y	Station	Sediment Depth cm	Sediment Porosity ml cm <sup>-3</sup>	Inst + NH <sub>4</sub> -N μM	Sediment Density g cm <sup>-3</sup>	Exc + NH <sub>4</sub> -N μM	Notes
6-26-76	B	0-5	0.75	71.6			
		5-10	0.63	205.0			
		10-15	0.58	154.7			
	B	0-5	0.75	87.3			
		5-10	0.63	242.7			
		10-15	0.58	148.4			
	B	0-5	0.81	22.3			
		5-10	0.76	3.5			
		10-15	0.66	110.7			
6-28-76	G	0-5	0.95	84.0			
		5-10	0.91	566.0			
		10-15	0.62	497.4			
	G	0-5	0.97	96.3			
		5-10	0.74	366.4			
		10-15	0.66	481.0			
	G	0-5	0.90	92.2			
		5-10	0.79	620.2			
		10-15	0.78	722.5			
	G	0-5	0.98	158.6			
		5-10	0.86	730.7			
		10-15	0.71	595.6			
7-13-76	A	0-5	0.82	16.5			
		5-10	0.82	20.6			
		10-15	0.48	24.8			
	A	0-5	0.79	11.3			
		5-10	0.71	14.4			
		10-15	0.57	32.0			
	A	0-5	0.81	15.4			
		5-10	0.77	12.3			
		10-15	0.53	32.0			
7-15-76	H	0-5	0.75	21.0			
		5-10	0.70	201.0			
		10-15	0.69	215.5			
	H	0-5	0.89	20.0			
		5-10	0.73	105.6			
		10-15	0.70	223.8			
	H	0-5	0.93	35.5			
		5-10	0.77	236.3			
		10-15	0.79	169.9			

Date M-D-Y	Station	Sediment Depth cm	Sediment Porosity ml cm <sup>-3</sup>	Inst NH <sub>4</sub> <sup>+</sup> -N μM	Sediment Density g cm <sup>-3</sup>	Exc NH <sub>4</sub> <sup>+</sup> -N μM	Notes
7-14-77	2	0-5		14.0			
		5-10		44.5			
		10-15		44.5			
	2	0-5		44.4			
		5-10		78.4			
		10-15		78.4			
7-14-77	4	0-5	0.61	40.9	1.29	27.6	Extracted
		5-10	0.55	63.6	1.67	54.5	with
		10-15	-	-	-	39.0	15 ml KCl
7-25-77	4	0-5	0.63	25.7	1.43	24.2	
		5-10	0.71	56.0	1.62	28.6	
		10-15	0.39	54.7	1.65	23.1	
	4	0-5	0.45	34.1	1.48	45.3	
		5-10	0.54	73.6	1.68	39.4	
		10-15	0.47	47.7	1.72	36.7	
7-13-77	7	0-5	0.72	74.2	1.21	42.6	
		5-10	0.67	75.8	1.34	34.9	
		10-15	0.70	40.6	1.46	36.4	
7-18-77	7	0-5	0.82	62.2	1.29	30.4	
		5-10	0.63	63.0	1.38	21.4	
		10-15	0.60	49.7	1.40	29.3	
	7	0-5	0.67	46.4	1.10	10.9	
		5-10	0.66	33.0	1.30	48.7	
		10-15	0.71	28.6	1.50	27.8	
7-13-77	10	0-5	0.85	59.2	1.18	15.1	
		5-10	0.92	55.8	1.38	25.9	
		10-15	0.95	228.6	1.47	40.9	
7-16-77	10	0-5	0.80	305.3	1.63	5.1	
		5-10	0.85	265.1	1.59	18.9	
		10-15	0.77	84.0	1.49	17.4	
	10	0-5	0.83	322.6	1.02	16.5	
		5-10	0.85	405.1	1.42	23.6	
		10-15	0.78	682.9	1.46	20.1	
7-30-77	15	0-5	0.80	305.5	1.20	69.5	
		5-10	0.80	617.4	1.25	110.6	
		10-15	0.71	1272.0	1.21	70.4	
	15	0-5	0.97	788.8	1.18	17.4	
		5-10	0.92	1386.3	1.27	46.0	
		10-15	0.82	1830.0	1.25	44.3	

Date M-D-Y	Station	Sediment Depth cm	Sediment Porosity ml cm <sup>-3</sup>	Inst NH <sub>4</sub> -N μM	Sediment Density g cm <sup>-3</sup>	Exc NH <sub>4</sub> -N μM	Notes
7-30-77	15	0-5	0.77	147.3	1.03	98.9	
		5-10	0.86	889.8	1.22	13.4	
		10-15	0.77	1307.2	1.43	42.2	
	15	0-5	0.94	516.4	1.14	18.6	
		5-10	0.99	1056.8	1.40	66.9	
		10-15	0.81	889.8	1.34	145.5	
6-5-78	1	0-5	0.90	18.6			
		5-10	0.65	22.9			
		10-15	0.55	32.0			
	1	0-5	0.86	24.7			
		5-10	0.84	-			
		10-15	0.54	29.2			
6-7-78	2	0-5	0.96	4.8			
		5-10	0.89	11.3			
		10-15	0.63	4.5			
	2	0-5	0.96	42.8			
		5-10	0.89	11.0			
		10-15	0.63	6.3			
6-9-78	4	0-5	0.72	18.8			
		5-10	0.57	9.1			
		10-15	0.42	9.1			
6-3-78	8	0-5	0.88	26.2			
		5-10	0.74	13.9			
		10-15	0.71	26.5			
	8	0-5	0.88	19.3			
		5-10	0.74	27.6			
		10-15	0.71	11.3			
6-12-78	9	0-5	0.87	26.5			
		5-10	0.75	169.1			
		10-15	0.69	61.2			
	9	0-5	0.87	38.7			
		5-10	0.75	96.9			
		10-15	0.69	142.3			
6-17-78	14	0-5	0.97	155.0			
		5-10	0.86	486.1			
		10-15	0.82	806.3			
	14	0-5	0.97	258.2			
		5-10	0.86	601.9			
		10-15	0.82	848.5			

Date M-D-Y	Station	Sediment Depth cm	Sediment Porosity ml cm <sup>-3</sup>	Inst NH <sub>4</sub> <sup>+</sup> -N μM	Sediment Density g cm <sup>-3</sup>	Exc NH <sub>4</sub> <sup>+</sup> -N μM	Notes
8-16-79	2D	0-5	0.70	32.7			
		5-10	0.55	27.1			
		10-15	0.50	16.5			
	2C	0-5	0.70	34.0			
		5-10	0.55	33.8			
		10-15	0.50	29.5			
8-10-79	2	0-5	0.75	72.3	1.48	316.8	Extracted
		5-10	0.62	27.5	1.80	49.5	with
		10-15	0.59	21.1	1.67	38.2	2 ml KCl
	2	0-5	0.65	40.0	1.42	169.8	
		5-10	0.50	35.5	1.48	44.9	
		10-15	0.46	15.1	1.68	35.7	
6-11-79	3	0-5	0.82	29.1	1.34	242.4	Extracted
		5-10	0.65	18.9	1.52	64.2	with
		10-15	0.55	14.9	1.52	46.4	4 ml KCl
	3	0-5	0.87	39.6	1.56	86.9	
		5-10	0.80	29.3	1.41	61.2	
		10-15	0.55	22.4	1.52	52.5	
6-16-79	3D	0-5	0.98	29.2			
		5-10	0.76	27.5			
		10-15	0.64	25.4			
	3C	0-5	0.91	43.6			
		5-10	0.78	46.3			
		10-15	0.63	36.5			
6-11-79	7	0-5	0.84	43.1	1.23	68.2	Extracted
		5-10	0.81	29.7	1.24	70.2	with
		10-15	0.75	24.1	1.43	44.9	4 ml KCl
	7	0-5	0.84	29.9	1.26	92.1	
		5-10	0.59	18.6	1.43	38.3	
		10-15	0.74	10.8	1.53	41.5	
6-16-79	7D	0-5	1.09	32.1			
		5-10	0.90	30.0			
		10-15	0.76	24.8			
	7C	0-5	0.96	29.2			
		5-10	0.84	32.1			
		10-15	0.78	61.2			

Date M-D-Y	Station	Sediment Depth cm	Sediment Porosity ml cm <sup>-3</sup>	Inst NH <sub>4</sub> <sup>+</sup> -N μM	Sediment Density g cm <sup>-3</sup>	Exc NH <sub>4</sub> <sup>+</sup> -N μM	Notes
6-10-79	8	0-5	0.82	25.1	1.39	153.7	Extracted with 2 ml KCl
		5-10	0.73	27.0	1.33	131.8	
		10-15	0.65	19.5	1.45	69.7	
	8	0-5	0.84	31.5	1.37	66.8	
		5-10	0.72	23.1	1.49	63.0	
		10-15	0.65	14.6	1.40	48.7	
6-14-79	8C	0-5	0.83	46.5			
		5-10	0.72	32.5			
		10-15	0.65	20.5			
6-14-79	8D	0-5	0.83	25.4			
		5-10	0.72	37.6			
		10-15	0.65	20.8			
6-11-79	9	0-5	0.92	38.4	1.39	46.4	Extracted with 4 ml KCl
		5-10	0.70	47.1	1.33	40.6	
		10-15	0.67	22.5	1.43	35.3	
	9	0-5	0.80	20.7	1.37	53.9	
		5-10	0.69	32.2	1.50	31.4	
		10-15	0.65	16.9	1.72	43.7	
	9C	0-5	0.84	31.1			
		5-10	0.66	52.6			
		10-15	0.61	20.3			
	9D	0-5	0.72	124.8			
		5-10	0.67	33.1			
		10-15	0.62	16.8			



Table D.2. Sediment organic content

Date M-D-Y	Station	Sediment Depth cm	Organic Content %
7-13-76	A	0-5	4.86
		5-10	3.26
		10-15	1.82
	A	0-5	7.45
		5-10	3.30
		10-15	2.54
	A	0-5	5.47
		5-10	3.51
		10-15	1.56
	A	0-5	5.67
		5-10	2.82
		10-15	1.58
7-15-76	H	0-5	5.65
		5-10	2.99
		10-15	2.90
	H	0-5	4.30
		5-10	3.60
		10-15	2.60
	H	0-5	5.38
		5-10	3.00
		10-15	2.97
7-5-76	B	0-5	6.99
		5-10	5.23
		10-15	4.50
	B	0-5	6.61
		5-10	4.17
		10-15	3.92
	B (sand)	0-5	0.91
		5-10	0.90
	B (sand)	0-5	0.85
		5-10	0.83
		10-15	0.88
	B (soil)	0-5	6.24
		5-10	4.85
		10-15	5.35
6-30-76	S	0-5	11.47
		5-10	6.56
		10-15	5.59

Date M-D-Y	Station	Sediment Depth cm	Organic Content %
6-30-76	S	0-5	9.94
		5-10	7.30
		10-15	5.55
	S	0-5	7.29
		5-10	4.72
		10-15	4.17
	S	0-5	8.14
		5-10	7.92
		10-15	5.97
6-28-76	G	0-5	7.31
		5-10	5.11
		10-15	5.26
	G	0-5	7.87
		5-10	7.97
		10-15	5.26
	G	0-5	7.95
		5-10	4.91
		10-15	5.78
	G	0-5	8.31
		5-10	6.47
		10-15	4.39
8-14-79	2	0-5	5.3
		5-10	2.1
		10-15	1.7
	2	0-5	4.1
		5-10	2.3
		10-15	1.3
8-14-79	8	0-5	7.6
		5-10	6.6
		10-15	4.6
	8	0-5	7.9
		5-10	4.8
		10-15	5.3
	8	0-5	6.9
		5-10	5.8
		10-15	4.8

## REFERENCES

- Aioi, K. 1980. Seasonal change in the standing crop of eelgrass (*Zostera marina* L.) in Odawa Bay, central Japan. *Aquat. Bot.* 8:343-354.
- Aioi, K. and H. Mukai. 1980. On the distribution of organic contents in a plant of eelgrass (*Zostera marina* L.) *Jap. J. Ecol.* 30:189-192.
- Aller, R. C. and J. Y. Yingst. 1980. Relationship between microbial distribution and the anaerobic decomposition of organic matter in surface sediments of Long Island Sound, U.S.A. *Mar. Biol.* 56:29-42.
- Aspinall, D. 1961. The control of tillering in barley plant. 1. The pattern of tillering and its relation to nutrient supply. *Aust. J. Biol. Sci.* 14:493-505.
- Backman, T. W. and D. C. Barilotti. 1976. Irradiance reduction: effect on standing crops of the eelgrass *Zostera marina* in a coastal lagoon. *Mar. Biol.* 34:33-40.
- Barsdate, R. J. and R. C. Dugdale. 1965. Rapid conversion of organic nitrogen of  $N_2$  for mass spectrometry: An automated Dumas procedure. *Anal. Biochem.* 13:1-5.
- Barsdate, R. J., M. Nebert, and C. P. McRoy. 1974. Lagoon contributions to sediments and water of the Bering Sea. In D. W. Hood and E. J. Kelley (eds.), *Oceanography of the Bering Sea*. Inst. Mar. Sci. Occas. Pub. No. 3, Univ. of Alaska, Fairbanks. p. 552-578.
- Bender, M. L., K. A. Fanning, P. N. Froelich, G. R. Heath, and V. Maynard. 1977. Interstitial nitrate profiles and oxidation of sedimentary organic matter in the Eastern Equatorial Atlantic. *Science* 198:605-609.
- Berner, R. A. 1977. Stoichiometric model for nutrient regeneration in anoxic sediments. *Limnol. Oceanogr.* 22(5):781-786.
- Blackburn, T. H. 1979a. Method for measurement rates of  $NH_4^+$  turnover in anoxic marine sediments, using  $^{15}N-NH_4^+$  dilution technique. *Appl. Environ. Microbiol.* 33(4):760-765.
- Blackburn, T. H. 1979b. Seasonal variation in the rate of organic-N mineralization in anoxic marine sediments. Colloque International C.N.R.S. Biogeochimie de la Matiere Organique a l'Interface Eau-Sediment Marin. Marseille, 25-27 April 1979.

- Brown, C. L. 1962. The ecology of aufwuchs on *Zostera marina* in Charlestown Pond, Rhode Island. M.S. Thesis, Univ. of R.I., Kingston. 52 p.
- Burkholder, P. R. and T. E. Doheny. 1968. The biology of eelgrass, with special reference to Hempstead and South Oyster Bays, Nassau County, Long Island, New York. Contr. No. 3, Dep. Conserv. and waterways, Town of Hempstead, L. I. (also, Contr. No. 1227, Lamont Geol. Observatory, Palisades, N.Y.). 120 p.
- Button, D. K. 1978. On the theory of control of microbial growth kinetics by limiting nutrient concentrations. *Deep-Sea Res.* 25(12):1163-1177.
- Capone, D. G., P. A. Penhale, R. S. Oremland, and B. F. Taylor. 1979. Relationship between productivity and  $N_2$  ( $C_2H_2$ ) fixation in a *Thalassia testudinum* community. *Limnol. Oceanogr.* 24(1):117-125.
- Carignan, R. and J. Kalff. 1979. Quantification of the sediment phosphorus available to aquatic macrophytes. *J. Fish. Res. Board Can.* 36:1002-1005.
- Carignan, R. and J. Kalff. 1980. Phosphorus sources for aquatic weeds: water or sediment? *Science* 207:987-989.
- Chapin, F. S., L. L. Tieszen, M. C. Lewis, P. C. Miller, and B. H. McCown. 1980. Control of tundra plant allocation patterns and growth. In J. Brown, F. L. Bunnell, P. C. Miller, L. L. Tieszen (eds.), *An Arctic Ecosystem: The Coastal Tundra of Northern Alaska*. Dowden, Hutchinson and Ross, Stroudsburg, Pa. p. 142-187.
- Clarkson, D. T. 1974. *Ion Transport and Cell Structure in Plants*. McGraw Hill. 350 p.
- Conover, J. T. 1968. The importance of natural diffusion gradients and transport of substances related to benthic plant metabolism. *Bot. Mar.* 6:1-9.
- Conover, J. T. and E. Gough. 1966. The importance of stem and leaf vs. root assimilation in *Ruppia maritima* L. and *Zostera marina* L. related to seasonal growth. Tech. Rep. III, WP-00023, NIH, Grad. Sch. of Oceanography, Univ. of R.I., Kingston, R.I. p. 6-1 through 6-19.
- Dennison, W. 1979. Light adaptation of plants: A model based on the seagrass *Zostera marina* L. M.S. Thesis, Univ. of Alaska, Fairbanks. 70 p.

- Doohan, M. E. and E. H. Newcomb. 1976. Leaf ultrastructure and  $\delta^{13}$  values of three seagrasses from Great Barrier Reef. *Aust. J. Plant Physiol.* 3:9-23.
- Drew, E. A. 1979. Physiological aspects of primary production in seagrasses. *Aquat. Bot.* 7:139-150.
- Dugdale, R. C. and J. J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.* 12: 196-206.
- Epstein, E. 1972. Mineral Nutrition of Plants: Principles and Perspectives. Wiley, N.Y. 412 p.
- Evans, L. T., I. F. Wardlaw, and C. N. Williams. 1964. Environmental control of growth. In C. Barnald (ed.), Grasses and Grassland, MacMillan, N.Y. p. 102-125.
- Fonseca, M. S. and G. W. Thayer. 1979. The effects of current velocity in a seagrass system. In Annual Report of the Beaufort Laboratory to the U. S. Department of Energy. Southeast Fisheries Center, Beaufort Laboratory, Beaufort, N.C. p. 203-229.
- Fried, M., F. Zsoldos, P. B. Vose, and I. L. Shatokhin. 1965. Characterizing the  $\text{NO}_3$  and  $\text{NH}_4$  uptake process of rice roots by use of  $^{15}\text{N}$  labelled  $\text{NH}_4\text{NO}_3$ . *Physiol. Plant.* 18:313-320.
- Gallagher, J. L. 1975. Effects of an ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus*. *Amer. J. Bot.* 62:644-648.
- Grundmanis, V. and J. W. Murray. 1977. Nitrification and denitrification in marine sediments from Puget Sound. *Limnol. Oceanogr.* 22(5): 804-813.
- Hale, S. S. 1976. The role of benthic communities in the nitrogen and phosphorus cycles of an estuary. In F. G. Howell, J. B. Gentry, and M. H. Smith (eds.), ERDA Symposium Series 1975. (CONF-740513). p. 291-308.
- Harrison, P. G. and K. H. Mann. 1975. Chemical changes during the seasonal cycle of growth and decay in eelgrass (*Zostera marina*) on the Atlantic coast of Canada. *J. Fish. Res. Board Can.* 32(5): 615-621.
- Hartog, C. den. 1970. The Seagrasses of the World. North Holland Publ. Co., Amsterdam. 275 p.
- Hassan, M. M. and T. V. Hai. 1976. Ammonium and potassium uptake by citrus roots. *Physiol. Plant.* 36:20-22.

- Haynes, R. J. and K. M. Goh. 1978. Ammonium and nitrate nutrition of plants. *Biol. Rev.* 53:465-510.
- Hopkinson, C. S. and J. W. Day. 1977. A model of the Barataria Bay salt marsh ecosystem. In C. A. S. Hall and J. W. Day (eds.), *Ecosystem Modeling in Theory and Practice: An Introduction With Case Histories*. John Wiley and Sons, N.Y. p. 235-287.
- Iizumi, H. 1979. The nitrogen cycling in eelgrass (*Zostera marina* L.) beds. Ph.D. Thesis, Univ. of Tokyo, Japan. 120 p.
- Iizumi, H., A. Hattori, and C. P. McRoy. 1980. Nitrate and nitrite in interstitial waters of eelgrass beds in relation to the rhizosphere. *J. Exp. Mar. Biol. Ecol.* 47:191-201.
- Jacobs, R. P. W. M. 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina*, at Roscoff, France. *Aquat. Bot.* 7:151-172.
- Joseph, R. A., T. V. Hai, and J. Lambert. 1975. Multiphasic uptake of ammonium by soybean roots. *Physiol. Plant.* 34:321-325.
- Keller, M. and S. W. Harris. 1966. The growth of eelgrass in relation to tidal depth. *J. Wildlife Mgt.* 30:280-285.
- Koroleff, F. 1976. Determination of  $\text{NH}_4^+$ -N. In K. Grasshoff (ed.) *Methods of Seawater Analysis*. Verlag Chemie, Weinheim. p. 127-133.
- Kremer, J. N. and S. W. Nixon. 1978. A Coastal Marine Ecosystem Simulation and Analysis. Springer-Verlag Berlin Heidelberg, N.Y. 217 p.
- Krom, M. D. and R. A. Berner. 1980. The diffusion coefficient of sulfate, ammonium and phosphate ions in anoxic marine sediments. *Limnol. Oceanogr.* 25(2):327-337.
- Kuo, J. 1978. Morphology, anatomy and histochemistry of the genus *Posidonia* König (Posidoniaceae). I. Leaf blade and leaf sheath of *Posidonia australis* Hook. f. *Aquat. Bot.* 5:171-190.
- Langer, R. H. M. 1966. Mineral nutrition of grasses and cereals. In F. L. Milthorpe and J. D. Ivins (eds.), *The Growth of Cereals and Grasses*. Butterworth, London. p. 213-226.
- Lipschultz, F., J. J. Cunningham, and J. C. Stevenson. 1979. Nitrogen fixation association with four species of submerged angiosperms in the central Chesapeake Bay. *Est. and Coast. Mar. Sci.* 9: 813-818.

- Lloyd-Jones, C. P., G. A. Hudd, and D. G. Hill-Cottingham. 1974. The determination of nitrogen-15 in plant material with an emission spectrometer. *Analyst* 99:580-587.
- Martens, C. S., R. A. Berner, and J. K. Rosefeld. 1978. Interstitial water chemistry of anoxic Long Island Sound sediments. 2. Nutrient regeneration and phosphate removal. *Limnol. Oceanogr.* 23(4): 605-617.
- Martens, C. S., G. W. Kipphut, and J. V. Klump. 1980. Sediment-water chemical exchange in the coastal zone traced by *in situ* radon-222 flux measurements. *Science* 208:285-288.
- McCaffrey, R. J., A. C. Myers, E. Davey, G. Morrison, M. Bender, N. Lvedtke, D. Cullen, P. Froelich, and G. Klinkhammer. 1980. The relation between pore water chemistry and benthic fluxes of nutrients and manganese in Narragansett Bay, Rhode Island. *Limnol. Oceanogr.* 25(1):31-44.
- McMillan, C. 1978. Morphogeographic variation under controlled conditions in five seagrasses, *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*, *Halophila engelmannii*, and *Zostera marina*. *Aquat. Bot.* 4:169-189.
- McRoy, C. P. 1966. The standing stock and ecology of eelgrass, *Zostera marina*, in Izembek Lagoon, Alaska. M.S. Thesis, Univ. of Wash., Seattle. 138 p.
- McRoy, C. P. 1970. Standing stocks and other features of eelgrass (*Zostera marina*) populations on the coast of Alaska. *J. Fish. Res. Bd. Canada.* 27:1811-1821.
- McRoy, C. P. 1973. Seagrass Ecosystems: Research Recommendations of the International Seagrass Workshop, Leiden, The Netherlands. 62 p.
- McRoy, C. P. 1974. Seagrass productivity: carbon uptake experiments in eelgrass, *Zostera marina*. *Aquaculture* 4(2):131-137.
- McRoy, C. P. unpublished. Data collected at Izembek Lagoon, Alaska, 1967-1975.
- McRoy, C. P. and R. J. Barsdate. 1970. Phosphate absorption in eelgrass. *Limnol. Oceanogr.* 15:6-13.
- McRoy, C. P. and J. J. Goering. 1974. Nutrient transfer between the seagrass *Zostera marina* and its epiphytes. *Nature* 228:173-174.
- McRoy, C. P. and C. Helfferich. 1977. Seagrass Ecosystems: A Scientific Perspective. M. Dekker Inc., New York, N.Y. 314 p.

- McRoy, C. P. and C. McMillan. 1977. Productivity and physiological ecology of seagrasses. In C. P. McRoy and C. Helfferich (eds.), *Seagrass Ecosystems: A Scientific Perspective*. M. Dekker Inc., New York, N.Y. p. 53-87.
- McRoy, C. P., R. J. Barsdate, and M. Nebert. 1972a. Phosphorus cycling in an eelgrass (*Zostera marina* L.) ecosystem. *Limnol. Oceanogr.* 17(1):58-67.
- McRoy, C. P., J. J. Goering, and W. E. Shiels. 1972b. Studies of primary production in the eastern Bering Sea. In A. Y. Takenouti *et al.* (eds.), *Biological Oceanography of the Northern North Pacific Ocean*. Motoda Shoten-Idemitsu, Tokyo. p. 199-216.
- McRoy, C. P. and M. J. Klug. unpublished. Data collected at Izembek Lagoon, Alaska, as part of the Seagrass Ecosystem Study, IDOE, 1975-1980.
- Milthorpe, F. L. and J. Moorby. 1974. *Introduction to Crop Physiology*. Cambridge Univ. Press, Great Britain.
- Mukai, H., K. Aioi, and Y. Ishida. 1980. Distribution and biomass of eelgrass (*Zostera marina* L.) and other seagrasses in Odawa Bay, central Japan. *Aquat. Bot.* 8:337-342.
- Murray, J. W., V. Grundmanis, and W. M. Smethie. 1978. Interstitial water chemistry in the sediments of Saanich Inlet. *Geochim. Cosmochim. Acta* 42:1011-1026.
- Nixon, S. W., C. A. Oviatt, and S. S. Hale. 1976. Nitrogen regeneration and the metabolism of coastal marine bottom communities. In J. M. Anderson and A. MacFadyen (eds.), *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*. Blackwell Scientific Publ., Oxford. p. 269-283.
- North, W. J. 1967. Integration of environmental conditions by a marine organism. In T. A. Olson (ed.), *Pollution and Marine Ecology*. John Wiley, N.Y. p. 195-224.
- Nye, P. H. and P. B. Tinker. 1977. *Solute Movement in the Soil-root System*. Univ. of California Press. 342 p.
- Nye, P. H., J. L. Brewster, and K. K. S. Bhat. 1975. The Possibility of predicting solute uptake and plant growth response from independently measured soil and plant characteristics. *Plant and Soil* 42:161-170.
- Olsen, S. R. and W. D. Kemper. 1968. Movement of nutrients to plant roots. *Advances in Agronomy*. 20:91-151. Academic Press, N.Y.



- Orth, R. J. 1977. Effect of nutrient enrichment on growth of eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. *Mar. Biol.* 44:187-194.
- Ostenfeld, C. H. 1908. On the ecology and distribution of the grass wrack (*Zostera marina*) in Danish waters. *Rep. Dan. Biol. Stn.* 16:1-62.
- Partiquin, D. G. 1972. The origin of nitrogen and phosphorus for growth of the marine angiosperm *Thalassia testudinum*. *Mar. Biol.* 15:35-46.
- Penhale, P. A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. *J. Exp. Mar. Biol. Ecol.* 26:211-224.
- Philip, G. 1936. An enalid plant association in the Humber Estuary. *J. Ecol.* 26(1):205-219.
- Phillips, R. C. 1972. Ecological life history of *Zostera marina* L. (eelgrass in Puget Sound, Washington). Ph.D. Thesis, Univ. of Wash., Seattle. 152 p.
- Phillips, R. C. 1980. Phenology and Taxonomy of Seagrasses. In R. C. Phillips and C. P. McRoy (eds.), Handbook of Seagrass Biology; An Ecosystem Perspective. Garland STPM Press, N.Y. p. 29-40.
- Phillips, R. C. and C. P. McRoy. 1980. Handbook of Seagrass Biology; An Ecosystem Perspective. Garland STPM Press, N.Y. 353 p.
- Pomeroy, L. R., L. R. Shenton, R. D. H. Jones, and R. J. Reimold. 1972. Nutrient flux in estuaries. In Nutrients and eutrophication. ASLO Special Symp. Vol. I. p. 274-291.
- Rasmussen, E. 1973. Systematics and ecology of Isefjord marine fauna (Denmark). *Ophelia* 11:1-495.
- Raymont, J. E. G. 1947. A fish farming experiment in Scottish Sea lochs. *J. Mar. Res.* 6:219-227.
- Reeburgh, W. S. 1967. An improved interstitial water sampler. *Limnol. Oceanogr.* 12:163-165.
- Rosenfeld, J. K. 1979. Ammonium adsorption in nearshore anoxic sediments. *Limnol. Oceanogr.* 24(2):356-364.
- Sand-Jensen, K. 1975. Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. *Ophelia* 14:185-201.

- Setchell, W. A. 1929. Morphological and phenological notes on *Zostera marina* L. Univ. Calif. Pub. Bot. 14:389-452.
- Short, F. T. 1975. Eelgrass production in Charlestown Pond: an ecological analysis and numerical simulation model. M.S. Thesis, Univ. of Rhode Island, Kingston. 180 p.
- Short, F. T. 1980. A simulation model of the seagrass production system. In R. C. Phillips and C. P. McRoy (eds.), Handbook of Seagrass Biology; An Ecosystem Perspective. Garland STPM Press, N.Y. p. 275-295.
- Short, F. T., S. W. Nixon, and C. A. Oviatt. 1974. Field studies and simulation with a fine grid hydrodynamic model - seagrass and circulation in Charlestown Pond. In An environmental study of a nuclear power plant at Charlestown, Rhode Island. Univ. of R.I. 33, VI-B, p. 1-27.
- Smart, R. M. and J. W. Barko. 1980. Nitrogen nutrition and salinity tolerance of *Distichlis spicata* and *Spartina alterniflora*. *Ecology* 61:630-638.
- Smith, G. W., S. S. Hayasaka, and G. W. Thayer. 1979. Root surface area measurements of *Zostera marina* and *Halodule wrightii*. *Bot. Mar.* 22:347-358.
- Snedecor, G. W. and W. G. Cochran. 1973. Statistical Methods. 6th ed. The Iowa State Univ. Press, Ames, Iowa. 593 p.
- Toetz, D. W. 1973. The kinetics of  $\text{NH}_4$  uptake by *Ceratophyllum*. *Hydrobiol.* 41:275-290.
- Vanderborcht, J., R. Wollast, and G. Billen. 1977. Kinetic models of diagenesis in disturbed sediments. Part 2. Nitrogen diagenesis. *Limnol. Oceanogr.* 22(5):794-803.
- Wada, E., T. Tsugi, T. Saino, and A. Hattori. 1977. A simple procedure for mass spectrometric microanalysis of  $^{15}\text{N}$  in particulate organic matter with special reference to  $^{15}\text{N}$ -tracer experiments. *Anal. Biochem.* 80:312-318.
- Watson, D. J. 1963. Some features of crop nutrition. In J. D. Ivins and F. L. Milthorpe (eds.), The Growth of the Potato. Butterworth, London. p. 233-247.
- Weigert, R. G. 1979. Modeling salt marshes and estuaries: progress and problems. In P. Hamilton and K. B. Macdonald (eds.), Estuarine and Wetland Processes. Plenum Press, N.Y. p. 527-540.

- White, J. and J. L. Harper. 1970. Correlated changes in plant size and number in plant populations. *J. Ecol.* 58:467-485.
- Yoda, K., T. Kira, H. Ogawa, and H. Hazumi. 1963. Self-thinning in overcrowded pure stands under cultured and natural conditions. *J. Biol. Osaka Cy Univ.* 14:107-129.